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THE MEANINGS OF COMPETITION

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INTRODUCTION

"Competition" has come to have at least four meanings in animal ecology, genetics and evolution. Some of these meanings are so ambiguous that the word has largely lost its usefulness as a scientific term. Worse still, it has resulted in much misunderstanding and confusion in some of the writings in these three fields. A clarification seems to be specially important at present because of the importance which some authors attribute to competition in determining both the numbers of animals (the ecological problem) and the perils of animals (the genetical problem) in natural populations.

To distinguish the four meanings of competition in common use, let us consider the environment of an animal as all those things or qualities which influence its chance to survive and reproduce. This is what matters for the purposes of animal ecology and genetics. We are then in a position to break down the environment of an individual animal, in the way suggested by Andrewartha and Birch (1954), into the following components:

Weather ..... (I)
Food ..... (II)
A place in which to live ..... (III)
The number of other animals of the same species ..... (IV)
The number of other organisms of different species
(a) non-predators which utilize the same resources (space, food etc.) ..... (V)
(b) non-predators which do not utilize the same resources ..... (VI)
(c) predators ..... (VII)

These components are numbered for reference in classifying the meanings of competition according to breadth of meaning. The first two components are self explanatory. The component "a place in which to live" refers, for example, to a tree-hole of a particular size, containing water of a particular pH with a particular content of organic matter, such as is necessary for the larvae of a tree-hole breeding mosquito to live in. The meaning of the other components will become clearer in the examples given below.

The various meanings of competition may be classified according to the number of components of environment which are included within the concept:

Meaning 1 (components: IV, V)
Meaning 2 (components: IV, V, VI)
Meaning 3 (components: IV, V, VI, VII)
Meaning 4 (components: I to VII)

MEANING 1. (COMPONENTS: IV, V)

Competition occurs when a number of animals (of the same or of different species) utilize common resources the supply of which is short; or if the resources are not in short supply, competition occurs when the animals seeking that resource nevertheless harm one or other in the process. This is the strict meaning of competition and the one which corresponds more closely to the etymology of the word, namely "together-seek." Nevertheless there are shades of meaning within this concept which are quite important to distinguish. For example, there is more than one meaning of "short supply." There may be an "absolute shortage" of food, or some other resource, by which is meant that not enough food or suitable places in which to live exist for all the animals present. Or there may be a "relative shortage" of food, even when plenty of food is available, if the animals seeking the resource choose to fight over the same morsel. Two birds may arrive at a carcass at the same time and fight for food even though there are enough other carcasses around for both of them. Further, a distinction can be made within this definition of competition, depending on whether the resource is the sort which is consumed when it is used (for example, food) or not (for example, nesting sites). Nicholson (1954) refers to the first as "scramble" and the second "contest." Examples of "contest" are provided by the aggressive behavior of some birds in seeking watch-posts or singing-places in tree-tops. *Phoenicurus phoenicurus* and *Muscicapa striata* fight for the possession of watch-posts suited to both species. Similarly the species *Sylvia communis* and *Emberiza citrinella* and *Saxicola torquata* in Hungary may fight for the possession of singing posts on the tops of prominent bushes in shrubberies (Udvardy, 1951).

An example of "scramble" is provided by Ullyett's (1950) experiments with blowfly larvae. These experiments also illustrate two ways in which non-predators utilising the same resource may influence each other's death-rates. The following summary of some of Ullyett's experiments is paraphrased from Andrewartha and Birch (1954, page 419). Ullyett reared the larvae of the two species of blowflies, *Lucilia sericata* and *Chrysomyia chloropyga*, on a limited quantity of meat. The number of newly hatched larvae placed on 140 grams of meat varied from 100 to 10,000. The death rate was measured for each species at each density, both when the species were reared separately and when they were reared together. When the two species were reared together, the experiments were started with equal numbers of each. So the comparison to be made is between the death-rates, of say, Lucilia when all the other animals in the meat are of the same kind and

when every second one belongs to a different species, in this case *Chrysomyia chloropyga.* Ullyett could find no evidence that either species interfered with the other in any way except that they both required exactly the same sort of food. The larvae of *C. chloropyga* in these experiments are non-predators that require to share the same food as *L. sericata* without interfering with it in any other way.

In a parallel series of experiments Ullyett compared *Lucilia sericata* with a different species *Chrysomyia albiceps*, with quite different habits. In these experiments the death-rate of Lucilia was much greater when half the other animals around it were *C. albiceps* than when all were of its own kind. As the densities of the populations increased, the death-rate among Lucilia increased until it reached 100 per cent, that is, none survived to become adult. Although *C. albiceps* undoubtedly needs to share the same food as *L. sericata*, this is a relatively unimportant part of its relationship to Lucilia. Ullyet observed that the larvae of *C. albiceps* attack and eat those of Lucilia. This happens to some extent when both populations are quite sparse but to an increasing degree as the densities increase. Despite these "predatory" habits, the larvae of *C. albiceps* are not to be considered strictly as predators because, in the absence of Lucilia, meat is still their chief source of food. They come into the environment of Lucilia chiefly as non-predators which interfere directly with Lucilia. In the first example one species affects the death rate of the other simply by using its food. The example illustrates what Park (1954) called the "exploitation" component of competition. But in the second example there was an additional direct interference of one species by the other. This is what Park (1954) called the "interference" component of competition. Both types of influence, exploitation and interference, account for high mortality in natural populations of *Lucilia sericata* in South Africa (Ullyett, 1950) and of *Lucilia cuprina* in Australia (Waterhouse, 1947).

An analogous example of direct interference of one species by another in a natural population is provided by Brian's (1952) observations on ants. In a cut-over pine wood *Myrmecia sp.* was unable to maintain itself long in the presence of *Formica sp.* because Formica attacked and destroyed the workers of Myrmecia. The interference of one species by another may take more benign forms, as for example when the humming bird *Calype anna* successfully prevents *Selasphorus sasin* from occupying its chosen territory simply by aggressive displays or by giving chase to the invader. (Pitelka, 1951). Such threats, though not mortally wounding the combatants, are effective in preventing one species from establishing itself in the area of another.

In most of the examples given so far, one species caused an increase in death-rate of the other. But the depressive effect of one species on the rate of increase of another may also be brought about by a decrease in the birth-rate or fecundity. For example, the fecundity of *Trisolium castaneum* was greatly reduced when it was crowded with adults of *T. confusum* as compared with crowding of its own adults. (Birch, Park and Frank, 1951).

All the above examples have been called competition by their authors, though some authors at the same time questioned whether competition was the best word to use (e.g., Ullyett, 1950, p. 117). This meaning is the strict meaning of competition accepted implicitly or explicitly by many ecologists. Other examples of its use will be found in the following references; Clements and Shelford, 1939, p. 159-60; Crombie, 1947, Allee et al, 1949, p. 656, Park, 1954, p. 180; Udvardy, 1951, p. 100 and 104; Andrewartha and Birch, 1954, p. 22.

Darwin has used the word "competition" in this strict sense also as the following quotations from "The Origin of Species" (p. 59, 1876 edition) suggest: "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera. We see this in the recent extension over parts of the United States of one species of swallow having caused the decrease of another species. The recent increase of the missel-thrush in parts of Scotland has caused the decrease of the song-thrush.... We can simply see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature; but probably in no one case could we precisely say why one species has been victorious over another in the great battle of life." In the last part of Chapter III he wrote "Animals come into competition for food or resources." When defining his meaning of the "struggle for existence" (in Chapter 3) Darwin made it clear that he regarded competition as just one of the many components of the "struggle for existence." He certainly did not regard the two terms as synonymous in the way in which we find them used by some modern evolutionists (see Meaning 4).

The concept of competition is also used in palaeontology, though naturally it is much more difficult in this field to adduce evidence of how one species may have aided in the extinction of another. In most examples it is a matter of conjecture. But sometimes evidence is sufficient to provide at least some suggestions as to what might have happened. For example, in writing of the invasion of South America in the Cenozoic by 15 families of North American mammals Simpson (1950 p, 381) says; "To a fauna already large and essentially complete or closed ecologically were added a large number of new forms from the new continent. The enrichment inevitably involved some duplication. No two forms of different origin can have been precisely and fully equal in their needs and capacities, but many were sufficiently similar to be in competition for food and in general, living space. Some native groups held their own and some invading groups became extinct, but some native groups disappeared and (as a rule) were replaced by invaders." As examples of the latter Simpson mentions the disappearance of the old native ungulates and the survival of ungulates of northern origin; many old native rodents became extinct; marsupial carnivores became extinct and placental carnivores survived. Simpson envisages a common demand for

similar resources of food and space by the northern and southern forms. And he implies that there was not enough food or space for all. Alternatively they interfered with each other in the process of seeking their common resources. So when a southern carnivore met a northern carnivore they may have fought over a common prey, the victor usually being the northern form. Or it is possible that the northern carnivore was simply able to produce more offspring and carry them through to maturity on a limited amount of food.

Simpson (1953 p, 300) quotes many examples from the fossil record of "two groups of similar adaptive type" which lived together for a time but subsequently one increased while the other decreased to extinction. In these examples he considers it probable that "Competition led to extinction of one group, although of course this may not really have been true in a given case." One of the best documented examples of this type is the replacement of multituberculates by rodents in North America in the early Cenozoic. He suggests that the success of the rodents was associated with their more mechanically efficient incisors, as compared with the multituberculates. If this were the vital factor in their success then we have to visualize a food shortage in which rodents were, in the long run, more successful in getting more than their fair share. The situation might be analogous to the "scramble" of blowflies in the cultures of Ullyett's experiments with *Lucilia sericata* and *Chrysomyia chloropyga* mentioned earlier.

Competition in the sense used in these examples causes (or is presumed to cause) an increased death rate and/or a decreased birth rate, of one of the species. And in the examples in which crowding was confined to members of one species alone, the effect was increased death rate or decreased birth rate of the population, or of certain genotypes in the population. But this may not always be so. Allee et al, (1949, p, 395) gave the following curious example of what they choose to call "cooperative competition." When undiluted with sea water the longevity of spermatozoa of sea urchins is longer than when diluted. Then oxygen consumption is less and their activity is less. "If the available space is much restricted, the competition for it results in an inhibition of movement, a lowering of the rate of oxygen consumption, and a conservation of essential diffusible materials; and all this is accompanied by a decided increase in longevity. Competition here has distinctly beneficial results for all the competitors; it is cooperative, as contrasted with being disoperative." In so far as space and oxygen are in short supply this example might be conceived to conform to the definition of competition at the beginning of this section. But its outcome is so different from all the other examples cited that one wonders whether it is wise to group it with them. The example illustrates the diversity of phenomena which can be given the same name. It would, of course be excluded by any definition of competition which required increased mortality with crowding (see for example Nicholson's usage in Meaning 3).

Within this first meaning of competition we have then various shades of meaning: "contest," "scramble," each of which in turn may be associated

with either an "absolute shortage" of resource or a "relative shortage" of resource. And within the meaning of "scramble" the depression of the rate of increase may be due to shortage of resource (that is, starvation if food were the limiting resource to be exploited) or direct interference of one species by the other. "Contest" invariably involves interference of some sort. Each of these situations has been studied in laboratory populations but there is a sparsity of quantitative data from natural populations. However it is now eminently clear that, as Park (1954) points out, prediction about the outcome of competition is a matter of empirical study rather than deduction. Park's (1954) experiments with flour beetles provide a nice demonstration of this point.

MEANING 2 (COMPONENTS: IV, V, VI)

In addition to the phenomena covered by the scope of our first meaning of competition, some authors include an additional item, namely the interference with one species by another (with consequent change in birth rate or death rate) even when there is no demand for a common resource of space or food. But they exclude predation in which one animal eats another for its main source of food.

The following two examples are summarised from the work of Lloyd, Graham and Reynoldson (1940) and Lloyd (1953) on the fauna of sewage beds in England. These beds contain a variety of organisms which have provided scope for some fine studies on the interrelationships of organisms in a more or less confined place. Adults of Psychoda lay most of their eggs near the surface of these beds where two other sewage-bed species are most abundant: Lumbricillus and larvae of Metriocnemus. Lumbricillus tends to pulverize the growth of algae on the surface of the beds. And eggs of the other two species which happen to be in the algae mass tend to be washed away to the bottom of the bed and then out in the effluent. In this way the activities of Lumbricillus reduce the number of the other two species which happen to be in the surface of the bed. In commenting on this the authors state that "the loosening effects of one organism on another are important in the competition." They regard this as an example of competition though the species concerned are not "competing" for any common resource.

Another example which I quote from Lloyd (1943) concerns the two species *Metriocnemus longitarsus* and *M. birticollis*, both of which lay their eggs in the surface of sewage beds. But quite often *M. longitarsus* emerges earlier than the other species and so its eggs are laid earlier, and by the time *M. birticollis* is laying its eggs the larvae of *M. longitarsus* are well established. Both sorts of larvae feed on the algae that encrust the stones on the surface of the bed. There is never any shortage of algae on which they feed. Neither larvae seek out the eggs and larvae of the other species, but any eggs or small larvae which happen to be on the algae which is being eaten will be devoured. When *M. birticollis* lays its eggs after the larvae of *M. longitarsus* are well established, it runs the risk of being killed by the

larger larvae of *M. longitarsus*. As a consequence *M. birticollis* may become quite scarce. Lloyd describes this as competition. In neither of these examples are the two "competing" species seeking a common resource in short supply. The second example may bear some resemblance to what happens in crowded cultures of the blowflies Lucilia and *Chrysomyia albiceps* (see above), where Lucilia destroys Chrysomyia by attacks on its larvae. But there are two important differences. The two species of blowflies seek a common resource in short supply and secondly Lucilia seeks out and destroys larvae of Chrysomyia; its destructiveness is deliberate and not accidental. Now if we are to call accidental destructiveness by the name of competition, then it would be just as logical to say that motor cars compete with *Homo Sapiens* because some men are killed in motor car accidents.

Different again is the following example of interference which Gause (1934) described as competition. When the wild carp, *Cyprinus albus* was introduced into lakes inhabited by *Schizothorax intermidius* in Russia, the latter species was gradually eliminated, largely because the carp eats the spawn of Schizothorax. Gause does not give enough details for us to be certain as to what happened. Whether the carp actively seeks out the spawn of the other species or whether this only occurs when the numbers of both species are high is not stated.

A general definition of competition which covers all the above examples is given by Elton and Miller (1954, p, 475) "Interspecific competition, in the more limited and correct use of the notion, refers to the situations in which one species affects the population of another by a process of *interference*, that is, by reducing the reproductive efficiency or increasing the mortality of its competitor." It will be noted that the definition makes no reference to a common resource. In this respect it is much broader than Meaning 1.

MEANING 3 (COMPONENTS: IV, V, VI, VII)

In addition to including the joint use of a common resource (IV, V), and "interference" of one species by another even when the interfering species do not utilize common resources (VI), some authors include "predation" in their meaning of competition. By predation we mean the use of one animal as the main source of food of another. Predation then includes "parasitism" in the special sense in which entomologists use this term.

This meaning of competition does not include other influences on birth rate and death rate such as the influence of weather or quality of food. The following quotation from Nicholson (1937, p, 103) illustrates this unusual meaning. "The reactions of natural enemies to population changes of their hosts must be regarded as a form of competition, for these reactions decrease the chance of survival of individuals of the host species when the density of the host species is increased, and this is the essential feature of competition in animal communities. Furthermore, competition for food and space, and the interaction of natural enemies and their hosts, can both be rep-

resented by the same fundamental formula and its corresponding exponential curve... but my remarks about natural enemies will indicate to you that I am using the word 'competition' in a somewhat wider sense than that in which it is usually used." Nicholson's criterion of competition which he gives in this and other papers (For example, Nicholson, 1953, p. 143) is that the chances of survival decrease as density increases. His definition necessarily excludes Allee's "cooperative competition" (see above) where crowding increased survival. But it includes predation, though it is difficult to conceive of any sense in which predator and prey can be said to compete. There is no sense in which they compete for a common resource.

MEANING 4 (COMPONENTS: I TO VII)

Here we have the broadest meaning of competition and the meaning which has least claim to any etymological correctness. Competition is synonymous with natural selection, that is, the differential survival or fecundity of different species, or genotypes of a species, due to the action of any component of environment. This use of competition is found in the writings of geneticists and evolutionists more than in those of ecologists. Nevertheless it was not the sense in which Darwin spoke of competition in The Origin of Species (see above). Schmalhausen (1949 p. 61) leaves us in no doubt that this fourth concept is what he means by competition when he writes "elements of competition for the preservation of existence and for propagation are always present among members of a species; they are expressed in struggles for food, with enemies and parasites, with severe climatic conditions, with hunger and disease.... In its active form individual competition corresponds to the usual concept of competition for means of subsistence and for propagation.... In its *passive form,* individual competition includes the struggle of organisms against harmful physical (climate) and biologic (predators, parasites) factors in order to protect their own lives and those of their progeny. In this case, competition does not disturb the interests of other individuals of the same population and is not sharpened by an increase in numbers." The inappropriateness of competition as a term for these phenomena is evident when we consider the extreme case of a lethal gene. Such a gene may make some phenotypes lethal at particular temperatures, for example. At these temperatures the organisms with the gene will tend to be eliminated. They die because their physiological constitution is not fitted to such temperatures, not because they were competing for anything.

There is another sense in which competition is used commonly in genetics and evolution. The different genotypes of a species may have different sexual activities; sometimes females have preferences for mating with particular males. The males are then said to compete for females (e.g. Bateman, 1948; Merrell, 1949; Reed and Reed, 1950). Reed and Reed (1950) found that when a white-eyed male and female of *Drosophila melanogaster* were kept for 24 hours in a vial with a red-eyed male and female both fe-

males tended to mate with red-eyed males. As a consequence of the selective preference of females there is a rapid increase in the frequency of red-eyed individuals when the two sorts of flies are cultured together in population bottles. In Reed and Reed's experiments the white-eyed individuals had completely disappeared by the 25th generation. Both the authors and Moody (1953, p. 396) in commenting on these experiments state that the white-eyed flies compete with the red-eyed flies. If we regard the female as a prize then there is a sense in which the white-eyed male is unsuccessful in "competition" for the prize though the two sorts of males do not in any sense "contest" for the prize; they do not battle over females as some of the higher animals are supposed to do. But this meaning of competition is different from the strict meaning of competition (Meaning 1) in the following respects. It is not dependent upon crowding or a shortage of resources. It takes place at quite low densities as well as at high ones. There is a peculiar sense in which the white-eyed males suffer from a shortage of suitable females since few females want them. But there is no way of relieving this shortage. They would presumably still be rejected in an infinite population of females. It is quite possible that the frequency of rejection would be less when there were many females and few males if uncopulated females were more receptive than recently copulated ones. If this were the case one might be inclined to include this example within the scope of the strict meaning of competition (Meaning 1) despite the differences already mentioned. My own preference in the matter is to avoid grouping this with the diversity of phenomena which might be strictly called competition and simply call it what it is namely, selective mating.

NATURAL SELECTION WITHOUT "COMPETITION"

The frequency of a genotype in a sexual cross-fertilizing population may be altered by selection which does not involve any shortage of common resources. The genotypes which have a high survival value and which contribute more offspring to the next generation will tend to "swamp" out other less fit genotypes. They will make greater contributions of genes to each successive generation. The greater contribution of a successful genotype may be associated with its higher mating activity, higher fecundity or higher survival. And these advantages may be quite independent of any shortage of resources of food or space. The lethality or semi-lethality conferred on their carriers by some genes are contingent upon components of environment such as temperature, moisture and the quality of food (for examples see Dobzhansky and Spassky, 1944; Dobzhansky, Pavlovsky, Spassky & Spassky, 1955; Dobzhansky, 1956, Da Cunha, 1951). Other genes are deleterious to their carriers in most environments in which the population lives. Genes which confer higher fitness than others will be multiplied and spread in the gene pool until the Mendelian population approaches in constitution its "adaptive norm" for the environment concerned. All this may happen without resources being in short supply. Competition in the strict ecological sense may not be applicable; natural selection may occur without it.

This is not to say that crowding between genotypes and shortage of resources of food and space do not influence their survival value. It simply emphasizes that differences in fitness exist even without such shortages of resources. The influence of shortage of resource, as a consequence of crowding, on the relative fitness of genotypes of a species, is another problem and one which has been little studied either in laboratory populations or in nature. Such studies as have been made are quite illuminating. Some genes confer greater fitness on their carriers (as compared with alternative genes or gene arrangements) at high densities when resources are in short supply. But they are at a disadvantage at low densities. Conversely other genotypes which are at a disadvantage at high densities have greater fitness at low densities. This has been demonstrated for *D. melanogaster* (Lewontin, 1955) and for *D. pseudoobscura* (Birch, 1955).

Natural selection between genotypes thus operates when the population is increasing and when resources may tend to become limiting, and also when the population is declining in numbers. Natural selection does not necessarily become more intense as population density increases, nor is it necessarily reduced as density falls. Sometimes the reverse occurs. An increase in density is not necessarily associated with reduction of amount of resource, nor is a fall in density necessarily associated with an alleviation of a shortage in resource. Many of the changes in numbers of animals from season to season or from one year to another have little to do with the amount of food or space available. The limit of resources may not be reached. Whether or not the limit will be reached sooner or later is a matter of dispute among ecologists. But the dispute need not concern us here, for we want to know what might happen in any fluctuation in numbers we happen to be interested in and not in hypothetical averages. An increase in numbers associated with a decrease in selection and consequent increase in variability seems to be what happened in the population of the butterfly *Melitaea aurina* observed by Ford (1945). The numbers increased because the environment became favorable and at the same time selection was slackened. With rising numbers genotypes of the species which have high fecundity become relatively more frequent in the population. Conversely as numbers of a species decrease, natural selection is not necessarily reduced. Very often the decrease is brought about by unfavorable weather. Those genotypes which are not resistant to heat or cold, or whatever the case may be, will perish, leaving a more homogeneous but resistant population. An example of this is provided by the observations of Thompson, Bell and Pearson (1911) on the decline in numbers during winter of the wasp *Vespa vulgaris* which was associated with a reduction in the wasp's variability.

DISTINCTION BETWEEN THE INFLUENCE OF ONE GENOTYPE ON THE NUMBERS OF ANOTHER WITHIN A MENDELIAN POPULATION AND THE INFLUENCE OF ONE SPECIES ON THE NUMBERS OF ANOTHER SPECIES

Differential selection between genotypes of a species may occur without food or space being limiting. This was illustrated in the previous

section. The same holds for selection between species. However it is necessary to make a distinction as between species and as between genotypes when we come to consider the way in which one sort of animal affects the numbers of another sort of animal. If we exclude predation and mutualism, then one species can only affect the numbers of another species when there is either an "absolute" or a "relative" shortage of resource such as food or space. The only exceptions seem to be the special types of "interference" of one species by another which were discussed under the second meaning of competition and the special case of threat discussed in the first meaning of competition. But one genotype can directly affect the numbers of another sort of genotype in the same Mendelian population, even when food and space are not short. It can do this by its greater sexual activity such as a higher mating rate or by selective mating. A species can only reproduce its own species but a genotype may produce others than its own kind. A homozygote which mates with a different homozygote produces all heterozygotes. A homozygote which mates with a heterozygote produces homozygotes and heterozygotes. This difference beyween species and genotypes of a species is quite an obvious one and yet it is sometimes lost sight of in arguments on competition.

There is a second aspect in which competition has a different relevance for ecology as compared with genetics. The ecologist is often unable to distinguish between genotypes within the species he studies. He measures abundance of the species as a whole and not its separate genotypes. Now even though competition in the strict sense of our first meaning may exist, the abundance he measures may not be related to the "intensity of competition." To put the emphasis on competition in such a case is beside the point. Consider a situation in which the number of birds in a wood is dependent upon the number of nesting sites in this wood. Provided the birds do not fight one another in seeking nesting sites, of which we may suppose there are not enough to go around, the number of birds in the wood will be the same as the number of nesting sites. It will be independent of the original number of birds seeking nesting sites and therefore of the "intensity of competition." A study of the "intensity of competition" will only become relevant when the investigator is able to distinguish between genotypes and wants to know the proportion of the different types of birds in the population. Examples of this sort have been discussed in more detail by Andrewartha and Birch (1954). This is another example of the different contexts in which ecologist and geneticist see competition, the one being more concerned with how many animals there are and the other with what kind of animal.

CONCLUSION

Some ecologists and geneticists have expressed doubts about the wisdom of using the one word competition to cover such a variety of phenomena as is included in its many meanings. The point becomes the more cogent when the meaning happens to bear little relation to the use of the word in everyday speech (see, for example, Thompson, 1939; Dobzhansky, 1950;

Ullyett, 1950; Andrewartha and Birch, 1954). Words can be obstacles to clear thinking. Ecology is unfortunately no exception to Shelling's statement, "In science as in life men are governed more by words than by clear concepts." One wonders for example if anything is to be gained by saying that the death of *Chrysomyia chloropyga* was due to competition with Lucilia when they were crowded in the same culture. This statement provides less information than the direct statement of what happened, namely that Chrysomyia larvae died from sheer starvation because there was not enough food for both species. And to say that red-eyed *Drosophila melanogaster* are successful in competition with white-eyed Drosophila tells less than the direct statement that the red-eyed flies increase in frequency in mixed populations because of the preference of females for red-eyed males.

It is not the purpose of this article to propose alternative ways of considering the variety of phenomena which have been called competition. Suggestions along these lines have been made elsewhere by Andrewartha and Birch (1954, p. 399). But whatever personal preferences we may have in this regard it remains important that when the concept of competition is invoked, the particular usage should be clearly understood and stated. This is especially necessary when it is claimed, as it is by some, that competition is centrally important in the dynamics of natural populations and in evolution. We should know what it is that is claimed to be so important. We may then be in a stronger position to investigate the claim. If we choose to retain the use of the word and give it a precise meaning for biology, then the first meaning we have discussed is the logical choice. The additional influences incorporated in the second meaning of competition might better be called simply "interference." As for the third meaning, the additional item is simply predation and might as well be called such. The fourth meaning is synonymous with differential survival and reproduction, and hence with natural selection. But the more logical approach to natural selection is to differentiate those factors which are selective in the first meaning of competition discussed in this article and those which are not. Sometimes the two will operate together. We would then choose to reverse Schmalhausen's scheme, and instead of calling natural selection competition, consider natural selection under two heads; natural selection with competition and natural selection without competition.

SUMMARY

The various meanings of "competition" in ecology, genetics and evolution are grouped into four main meanings which differ in important respects from each other. They grade from a strict meaning to one so broad as to be synonymous with natural selection. In the strict sense competition between animals occurs when a number of animals (of the same or of different species) utilize common resources the supply of which is short; or if the resources are not in short supply competition occurs when the animals seeking that resource nevertheless harm one or another in the process.

Intermediate between the strict and the broad meanings are two others. One includes any interference of one species by another irrespective of

whether they use common resources or not, and the other includes predation within the meaning of competition. Each of the four meanings of competition is illustrated with examples.

A distinction is made between the influence of one species on the numbers of another and the influence of one genotype on the frequency of another genotype of the same species. In the former case one species can influence the frequency of another by competition only when there is a shortage of some resource. The one exception is some special cases of threat. The conclusion is drawn that if the term competition is retained in biological writings it should be restricted to the one strict meaning defined above. On the other hand this may be an appropriate time for approaching the problems of how one organism influences the numbers of another in a fresh way without recourse to the concept of competition at all.

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LITERATURE CITED

Allee, W. C., Emerson, A. E., Park, T., Park, O., and Schmidt, K. P., 1949, Principles of animal ecology. Philadelphia: W. B. Saunders Co.

Andrewartha, H. G., and Birch, L. C., 1954, The distribution and abundance of animals. University of Chicago Press, Chicago.

Bateman, A. J., 1948, Intra-sexual selection in Drosophila. Heredity, 2: 349–368.

Birch, L. C., 1955, Selection in *Drosophila pseudoobscura* in relation to crowding. Evolution, 9: 389–399.

Birch, L. C., Park, T., and Frank, M. B., 1951, The effect of intraspecies and interspecies competition on the fecundity of two species of flour beetles. Evolution, 5: 116–132.

Brian, M. V., 1952, The structure of a natural dense ant population. J. Anim. Ecol. 21: 12–24.

Clements, F. E., and Shelford, V. E., 1939, Bioecology. New York: John W. Wiley and Sons.

Crombie, A. C., 1947, Interspecific competition. J. Anim. Ecol. 16: 44–73.

Cunha, A. B. da, 1951, Modification of the adaptive values of chromosomal types in *Drosophila pseudoobscura* by nutritional variables. Evolution, 5: 395–404.

Dobzhansky, Th., 1950, Heredity, environment and evolution. Science, III: 161–166.

1956, A review of some fundamental concepts and problems of population genetics. Cold Spring Harbor Symposium (In Press).

Dobzhansky, Th., and Spassky, B., 1944, Genetics of natural populations XI. Manifestation of genetic variants in *Drosophila pseudoobscura* in different environments. Genetics, 29: 270–290.

Dobzhansky, Th., Pavlovsky, O., Spassky, B., and Spassky, N., 1955, Genetics of natural populations. XXIII. Biological role of deleterious recessives in populations of *Drosophila pseudoobscura*. Genetics, 40: 781–796.

Elton, C. S., and Miller, R. S., 1954, The ecological survey of animal communities with a practical system of classifying habitats by structural characters. J. Ecol. 42: 460–496.

Ford, E. B., 1954, Butterflies. London: Collins.

Gause, G. F., 1934, The struggle for existence. Baltimore: Williams and Wilkins.

Lewontin, R. C., 1955, The effects of population density and composition on viability in *Drosophila melanogaster.* Evolution, 9: 27–41.

Lloyd, L., 1943, Materials for a study in animal competition. II. The fauna of the sewage beds. III. The seasonal rhythm of *Psychoda alternata,* Ann. App. Biol. 30: 47–60.

Lloyd, L., Graham, J. F., and Reynoldson, T. B., 1940, Materials for a study in animal competition. The fauna of sewage beds. Ann. App. Biol. 27: 122–150.

Merrell, D. J.. 1949, Selective mating in *Drosophila melanogaster. Genetics,* 34: 370–389.

Moody, P. A., 1953., Introduction to evolution. New York: Harper and Brothers.

Nicholson, A. J., 1937, The role of competition in determining animal populations. J. Counc. Sci. Ind. Res. (Australia) 10: 101–6.

1953, The balance of animal populations. J. Anim. Ecol. 2: 132–178.

1954, An outline of the dynamics of animal populations. Aust. J. Zool. 2: 9–65.

Park, T., 1954, Experimental studies of interspecies competitions. II. Temperature, humidity and competition in two species of *Tribolium.* Physiol. Zool. 27: 177–238.

Pitelka, F. A., 1951, Ecologic overlap and interspecific strife in breeding populations of Anna and Allen humming birds. Ecology, 32: 641–661.

Reed, S. C., and Reed, E. W., 1950, Natural selection in laboratory populations of Drosophila. II. Competition between a white-eye gene and its wild type allele. Evolution, 4: 34–42.

Schmalhausen, I. I., 1949, Factors of evolution; the theory of stabilizing selection. Philadelphia: The Blakiston Co.

Simpson, G. G., 1950, History of the fauna of Latin America. Amer. Scientist, 38: 361–389.

1953, The major features of evolution. Columbia University Press. New York.

Thompson, W. R., 1939, Biological control and the theories of interactions of populations. Parasitology, 31: 299–388.

Thompson, R. J., Bell, J., and Pearson, K. 1911, A third cooperative study of *Vespa vulgaris.* Biometrika, 8.

Udvardy, M. D. F., 1951, The significance of interspecific competition in bird life. Oikos, 3: 98–123.

Ullyett, G. C., 1950, Competition for food and allied phenomena in sheep-blowfly populations. Phil. Trans. Roy. Soc. London. B. 234: 77–174.

Waterhouse, D. F., 1947, The relative importance of live sheep and of carrion as breeding grounds for the Australian sheep blowfly *Lucilia cuprina.* Bull. Counc. Sci. Ind. Res. Australia, No. 217.

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ASPECTS OF AGGREGATION IN CELLULAR SLIME MOULDS

1. Orientation and Chemotaxis

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In all spheres of biology we are concerned with the orientation of units—be they molecules, cells, organisms, or groups of these—in relation to other similar units and to the general environment, including larger units. We have first to describe their orientation as a behavioral response and then to account for it in terms of their other properties.

At the lowest level, we find that a molecule can influence the orientation of its close neighbors by means of various intermolecular forces, and they in their turn can do the same to theirs. The resultant two- and three-dimensional arrays are ubiquitous in protoplasm and its derivatives (Frey-Wyssling 1953). Their development has been invoked to explain cell differentiation (Weiss 1947); and it has been suggested (Wigglesworth 1948) that even a whole multicellular organism may be usefully considered to be a giant 'molecule'.

As molecules outside such an array (or the electric field commonly associated with biological systems) move at random, their individual paths cannot convey any directional information. Yet specific molecules can influence the orientation of a larger unit in various ways. If they are associated with a solid substratum, they may mark out a path, which should not be much wider than the unit that uses it, unless additional guidance is available; or they may label some fraction of existing pathways. They may be bound to the substratum so intimately that they may to some extent constitute an array, as in specific guides for nerve-fibre growth, and theoretically their orientation could give the path polarity. Or their association may be much looser, as in a scent trail. This could be polarized by a gradient along it, determined by the relative speeds of laying and disappearance; but if it were far outweighed by local differences in deposition, absorption, and loss, there would be no advantage in the pursuer's being sensitive enough to detect it. A hound running back on the scent reminds us that in the absence of polarization (or alternative guidance) a respondent has no means of telling which way to move along the path.

If the molecules are free in a fluid, they can produce an effect in one of two ways. Firstly, in their presence, the unit may respond differently to any other guidance mechanism, of which a current is a rather special example, because it itself may carry the molecules, and indeed may do so for distances much greater than those over which diffusion gradients can effec-

tively operate. "Without convection currents, either spontaneous or self-induced, it is unlikely that insects could orient to odors at all"—Dethier (1947). Sensitivity can in theory be increased till a single molecule is able to initiate a response; and this ultimate limit must actually be approached in the case of some male moths.

Secondly, there may be differences in concentration, which may lead to unoriented accumulation by influencing the speed of movement or, if the responding unit has a certain ability to adapt to the stimulus, the total rate of undirected turning. Orientation—chemotaxis and chemotropism proper—can occur in a gradient that is flat in relation to the unit's powers of discrimination, if the unit has some form of memory and, on the basis of the concentration differences it experiences, is able to choose between the undirected sampling turns it has made. For guided turning, the gradient must be steep enough for different parts of the unit to be stimulated differentially (Fraenkel and Gunn, 1940). Regardless of the sensitivity of the response mechanism, the significance of the local distribution of the molecules must decrease as the differentials and the absolute numbers available for judgement fall.

The chemical can show all degrees of specificity upwards from that of the hydrogen ion, through simple metabolic products and injurious substances, to molecules that are uniquely involved in the response of a single species of unit.

SLIME-MOULD AGGREGATION

Because of the inherent limitations of chemotaxis and the technical difficulties of deciding whether it is involved in accumulation at specific points, its biological importance has been alternately exaggerated and dismissed. But it is not my purpose here to assess the extent to which biological orientation in general depends on chemical gradients; instead I shall consider the problems one group of organisms, the cellular slime moulds or Acrasiales, has faced in relying on such a mechanism.

In the family Dictyosteliaceae, which shows the most interesting life cycle (Olive 1902; Raper 1940a, b, 1941; Bonner 1944a), there are two genera, Dictyostelium and Polysphondylium, available to us for study. During the vegetative phase, their amoebae lead a solitary existence; they feed on bacteria, divide and move independently. In culture they can be maintained indefinitely in this phase (Potts 1902). Some time after the available food has been consumed, they begin to co-operate in their hundreds, and hundreds of thousands, in the erection of aerial fruiting bodies. As a first step in this process, some of the amoebae begin to act as collecting centers; and the others are attracted towards them, joining up as they go to form approximately radial streams, which grow coarser as they age and the finer branches flow into one another. At no time is a plasmodium formed: all the cells remain distinct. After aggregation, the resultant cell masses elongate and in time are borne up into the air on the stalks they

make by invagination of the leading cells; the remaining cells differentiate into spores.

The problem of why amoebae cease to move at random and aggregate towards centres has interested many workers (See Shaffer 1956a); but Bonner (1947) was the first to produce convincing evidence that they oriented to a gradient of a chemical, which he named *acrasin.*

Amoebae able to respond to centers will not move towards blocks of agar on which even large numbers of them have rested for varying periods, nor will they collect at the tips of capillary tubes containing various extracts of centres or the water that has bathed them (Shaffer 1953). It may be concluded either that a center imposes some further characteristics on the chemical signal or that secreted acrasin rapidly becomes inactive; if it were merely volatile, one might expect to get positive reactions to the capillary tubes, as did Cooke, Elvidge and Heilbron (1948) working with Fucus sperm.

Would the organism gain any advantage by inactivating it? If we assume that however great the absolute concentration is made there is a certain minimum percentage difference an amoeba can detect, the range from which it could be attracted to a point source of stable chemical in a large volume of medium would be strictly limited, as the steady-state relative concentration gradient would not be influenced by the amount of chemical secreted. But if the chemical were inactivated in a suitable way, the relative gradient at any distance could be increased, though the concentration would be lowered. The more rapid the inactivation, the greater the effect. A source could thus increase its range indefinitely, in theory; but in practice the limit would soon be reached, because the price of having to secrete more chemical, and of having to wait longer before the cells furthest away responded, would rise so enormously as the range was extended.

If the medium is actually limited in extent, or if it is effectively limited by the presence of other sources, inactivation is essential if a source is to maintain any range at all for long periods: this is simply a question of checking the growth of the background against which the gradation has to be detected. This need can be visualized by dropping a particle of dye into still water: one finds it progressively more difficult to judge where the particle is by examining, through a mask, part of the area coloured by diffusion; and the smaller the volume of liquid, the more rapidly does this happen.

Slime moulds can in fact aggregate on a bare glass surface in a damp atmosphere, in which conditions the volume of medium must be extremely small. Further, under even a shallow layer of water they are prevented from building fruiting bodies (Potts 1902), and instead they go through alternate phases of aggregation and dispersion for several days in the same medium. All this suggests that the secreted chemical is inactivated.

It may be noted, though, that if the reacting cells can remain oriented for some time after they have temporarily ceased to receive positive guidance from a chemical gradient, a source can maintain effective guidance

with a *stable* chemical for longer periods if it releases it not at a constant rate but in pulses at appropriate intervals. Even if the chemical were impermanent, it would be more efficient to do this. The possibility of there being such pulses in aggregation is brought to mind by the time-lapse films of this process taken by Arndt (1929, 1937) and Bonner (1944b), which show waves of rapid inward movement spreading outward from the centre, although Bonner's film and others taken by myself make it clear that such waves are not always present.

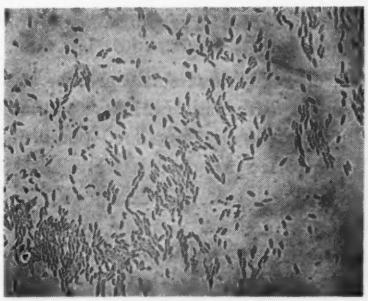
Whether the chemical is inactivated or fluctuation of the gradient is essential for stimulation, amoebae sensitive to the chemical should be able to orient to an artificial source that can be renewed at frequent intervals with the liquid obtained from the immediate vicinity of a natural source only a few seconds before. If a drop of this liquid, freed from cells, is added all round the edge of a block of agar a few millimeters square, resting on a glass slide, any acrasin it contains can reach amoebae sandwiched between the block and the slide only by diffusion; and fresh liquid can be added without mechanically disturbing the existing gradient. When this is done every minute, it is found that after about 10 minutes, the sensitive amoebae have turned, elongated, and begun to move more or less perpendicularly towards the nearest edge of the block (Shaffer 1953). Those close to a corner adopt an intermediate orientation and so form a pattern not unlike a quadrant of a natural radiate aggregation, but inside out—the artificial 'center' being at the periphery.

Acrasin solution as collected, even if cell-free, is inactivated within a few minutes at room temperature, due to the presence of an extracellular protein. If this is removed, acrasin is remarkably stable (Shaffer 1956a). The addition of a drop of its solution to the edge of a test agar block but once—and so a single acrasin pulse—is sufficient to bring about the orientation of the amoebae in two to three minutes (Fig. 1). As there are unlikely to be separate sensory, transmitting, and effector systems, it is probable that acrasin acts directly on the cell surface at the front end of an amoeba and causes a differential outflow of cytoplasm.

The following analysis is based on a recent series of papers (Shaffer 1956 a-d). Even at the periphery of an aggregation several centimeters across, an amoeba must be able to detect a difference in concentration at points only about 10 μ apart. Whatever its sensitivity and however acrasin were inactivated, far less time and chemical would be needed to establish an adequate gradient if the center were not the sole secretor but were helped by a series of boosters. In fact, as Bonner (1949) concluded from the observation that amoebae did not crawl straight towards the center but condensed into streams on their way there, streams do secrete acrasin. What has to be explained now is what ensures that the amoebae reach the center at all, or in other words, what makes the boosters carry the center's message rather than their own.

It has been assumed in the past (Arndt 1937; Bonner 1949; Sussman 1954) that the center controls aggregation (i) because of the number of

cells accumulated there and/or (ii) because these cells are specially active in producing the attractant. Let us consider the first explanation. Amoebae before aggregation move at random; and it has been suggested that if they then all began to make acrasin, centers would develop where they happened locally to be closer together. However, if all of them did suddenly start to secrete at about the same concentration, one would expect them to form small clumps all over the field, which would grow by irregular fusion till they were out of range of one another. This would be something like gravitational condensation, though it would be modified by the cells being polarized and by their adhering on contact which would tend to limit their direction of movement, and by their ability to change



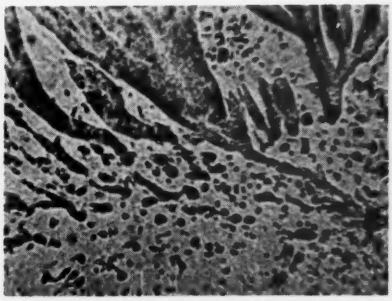


FIGURE 1. Amoebae of *Dictyostelium discoideum* lying under a block of agar and moving 'downwards' to the nearest edge of the block. 3 minutes after adding a drop of concentrated acrasin solution to the edge. × 80.

FIGURE 2. Amoebae of *Dictyostelium discoideum* streaming from an area where the cell density is high towards a centre (extreme right) that has formed where it is low. × 35.

speed, so that if one clump came to rest it would collect the others in the neighbourhood. But aggregation is not like this: the cells move towards the centre, broadly speaking, along radial pathways.

Further, if the food supply is unevenly distributed, the cells in an area where there is much available will multiply extensively; but they may find when they are ready to aggregate, that the center to which they are attracted has already formed in a neighboring sparser area. If this small center's influence depends on its size alone, one cannot explain how it remains the goal of streams that become thickest at their outer ends and taper steadily towards it (Fig. 2).

It might be supposed then that for the center to have much greater powers of secretion per cell than the periphery is both necessary and sufficient for aggregation to be radial. Actually it is neither. The influence of the chemical released by the center must fall off rapidly with increasing distance simply because of the shape of the diffusion gradient; and it must be so much further devalued by the output of the boosters, and by the higher

degree of inactivation their use demands, that it cannot possibly directly dominate the whole of an aggregation. As there must then be some other basis for centripetal movement in the outer part, one may suppose that the same mechanism is at work nearer the center, an area of much the same appearance. In short, if the center's secretion cannot dominate the gradient throughout an aggregation, there would seem to be no advantage in its dominating it anywhere except in the center's immediate vicinity. Thus, there is no point in the center's producing continuously or intermittently a much higher concentration than the periphery ever does (unless its inactivated acrasin is essential to the latter as a raw material—an improbable biochemical specialization). In fact, when there are no cells intervening, a center can attract cells from only about the same distance as a stream can—a mere few hundred micra—and direct comparison by Bonner's (1949) method shows that a center and a stream do secrete acrasin at something like the same concentration.

However, if the concentration at the center were fractionally greater than that in the part of the stream adjacent to it—a difference perhaps too small for his method to detect—and if this difference were continued out along the stream as a gradient of secretion, controlled so that it were not for most of the way far steeper than the amoebae needed, this could well provide guidance for much greater distances than could a gradient in the external medium. Yet, using another of Bonner's (1949) methods, no gradient in the amount of acrasin escaping from the sides of a stream is detectable; moreover, cells in a continuous compact stream do not usually turn towards a center transplanted close beside it.

Still, gradient guidance could operate even if the locus of highest concentration were not the center: if zones of temporarily increased acrasin secretion spread centrifugally along the streams—as is likely involved in producing rhythmic movement—they could expose the cells to adequate gradients as they reached them; and the reverse gradients after they had passed would not necessarily have an equal and opposite effect. But though perhaps such pulses do sometimes play a part in keeping stream cells oriented, they are probably neither essential nor constantly present. The absence of photographically recordable rhythms from some aggregations suggests this, though it is not conclusive. There is also the observation that when amoebae of one member of certain pairs of species are attracted to a stream made by the other member, the separate stream that they form alongside it, because surface differences prevent them from coalescing with it, can flow in either direction. Thus, when the first foreign cells reach the original stream, they cannot experience an acrasin gradient, of any kind, adequate to make them turn towards the center, though, of course, their sensitivity may be different from that of the cells in this stream. It is most likely that after these first foreign arrivals have made an undirected turn, the later ones adopt the same orientation by a contact reaction.

Whereas the separate cells before they have entered an aggregation do not secrete acrasin and have such a low degree of intercellular stickiness

that, in most species, they separate freely again after they have come in contact, the cells in streams and centers do secrete and are highly sticky—a property that is the basis for the mechanical strength of these structures. If it is assumed that the stimulus that induces the first type of cell to develop the properties of the second—a change that can be called integration—is contact with the second type, it is possible to explain why aggregation should be radiate even in the absence of quantitative dominance by the center. Cells that initiate centers by secreting acrasin would attract the neighboring cells towards them; only when these had made contact with them and founded the streams would they begin to secrete and attract the cells beyond them, and only when these had stuck on to the incipient streams and were guided by the flow therein rather than by the chemical gradient would they in their turn begin to secrete.

The development of aggregations in *Polysphondylium violaceum* appears to bear out this scheme. Centers are first visible as small clumps without any streams, and the latter then extend progressively outwards from them. Usually no streams form that are not from the beginning joined to the main system. Still, this does not prove that a cell must make contact with integrated cells for it itself to become integrated: it might be that it is stimulated to do so at some distance from the stream or center to which it is moving, but that it takes as long to change as it does to reach it. Though this may seem to be an unnecessarily complicated arrangement, it has been found to be operative. If the unintegrated cells are attracted towards a center that is dragged away as they move towards it, they will in due course form a compact, sticky, acrasin-secreting stream, without ever making contact with it. It is acrasin itself that induces integration.

Bonner derived the name *acrasin* from the Acrasiales, but he also had in mind the witch Acrasia in *The Faerie Queene* (Spenser 1590). In the Bowre of Blisse was to be found this

> *. . . . faire Witch her selfe now solacing,*
> *With a new Lover, whom through Sorceree*
> *And witchcraft, she from farre did thether bring.*

She was by no means content with merely attracting travellers; and after she had had her way with them, the untutored eye failed to recognize her hangers-on for what they had been:

> *. . . . these seeming beasts are men indeed,*
> *Whom this Enchauntresse hath transformed thus.*

It is thus most apt that acrasin has now been found not only to attract cells but also to alter their shape, surface, and other properties. It would be yet more fitting if sexual union were the basis of aggregation, as Wilson (1952, 1953) has indeed claimed; but so many workers on these organisms (Sussman 1954; Shaffer 1956d; see Wilson for earlier references) have failed to obtain evidence for this that we should scarcely be justified in likening the culture plate to the Bowre of Blisse.

Although contact is not the stimulus for integration, in *P. violaceum* the relationship between the distance at which the actual stimulus is re-

ceived, the time taken for this change to happen, and the speed of movement, is such that in the absence of experimental interference the cells will usually have reached the stream and be subject to flow guidance before they begin to secrete. This still provides an adequate explanation of why aggregation should be radial. However, it is common in some other species, including *Dictyostelium discoideum,* for an aggregation when it first appears to consist not of continuous compact streams but of diffuse expanses of cells, many of which are oriented though they are not in contact. From the extent of these 'stippled' aggregations, and from the sweep of the stream areas that results in the general orientation being in places directly away from the center, it is clear once again that the center is not even the main acrasin secretor. Yet though they are all releasing acrasin, the separate cells within the aggregation do not, by and large, unless they are disturbed, turn towards the cells beside them: they tend to remain pointing in the direction from which orientation spread and eventually to condense into definitive streams that are radial. The explanation appears to be that the effect of orientation, a process that involves turning and elongation, is, on average, to bring the front end of a cell closer to the cell that first attracted it than to any other; and only after this has happened does it secrete maximally. If the resultant attraction then acted through the centers of the cells, as it would do if aggregation were gravitational, it would not show a directional bias. It is because the gradient is measured at the front end that there is a higher probability that this resultant will be in the direction from which orientation spread rather than another. Closer examination of such an aggregation shows that orientation is only in general radial and that local divergence is common. That orderly aggregation does depend on the time relationship between orientation and secretion is shown by disturbing this experimentally: aggregation then becomes chaotic.

Though nothing is yet known about the pattern of emission by a single amoeba, it may be pointed out that if it released acrasin at the same concentration all over its surface, there would be a bigger gradient leading up to its highly curved rear end than to its sides, simply because of its shape. This difference might be of importance to the cells of low sensitivity in an early aggregation and be one of the factors helping them to join up end to end. Similarly, diffusion cannot produce anything like as great a relative concentration gradient near the surface of an aggregate of a few thousand cells as it can near a single secreting cell or a small clump of them. This may explain the observation that cells just beginning to turn into a stippled aggregation, and therefore guided by acrasin, may yet not respond to an aggregated cell mass that happens to migrate over them; though perhaps half an hour later, and especially if they are first disoriented, they will do so. Paradoxically, for a brief period while sensitivity develops, it may be that a source can be too big to be attractive.

It is suggested that centers owe their position not to their constantly secreting *more* than the peripheral cells but to secreting *before* them; and

this is due primarily to the ability of the cells that initiate the centers to release acrasin into the surrounding medium when there is either none there or not enough to bring about orientation. But their position is not then completely assured, and especially in the early stages of some species, a field of amoebae may successively enter different organizations (Arndt 1937; Raper 1940a). Arndt attributed this to changes in strength of the stimuli produced by the centers.

Probably these reorientations are best considered as special cases of rhythmic activity. In this, zones where the cells are moving more rapidly towards the center spread out from it. In one very slow and coarse form—the 'fairy ring' pattern of *P. violaceum* (Shaffer 1956d)—the cells between the fast zones actually lose their integration and wander about at random. The corresponding cells in the quicker and more delicate rhythms sometimes revealed by time-lapse films suffer a less extreme change of state, the only visible alteration being in their speed of movement. That these rhythms may embrace cells that are not in contact makes it probable that acrasin plays a part in their generation; but it is not yet possible to choose between the numerous hypotheses that would account for them, because the temporal course of a cell's secretion and velocity changes, if any, in response to acrasin are unknown. By using acrasin solutions to provide stimuli of known characteristics, one should be able to obtain the necessary information. For the present, it seems clear that when cells are moving alternately quickly and slowly in time with their neighbors, they are stimulated, discharge, recover, and then are stimulated again. It might be, for example, that acrasin reaching the external surface of a cell alters it so that there follows a greater outflow of both cytoplasm and acrasin. The subsequent slowing down must be due to fatigue or adaptation of one or more of the receptor, secretory, or motor systems (in so far as they are separable). In a stippled aggregation, in which the cells cannot yet avail themselves of flow guidance, it must be especially useful for the center to be able to reinforce its authority by repetitively re-exciting to some degree the acrasin relay system—'adaptation', among other factors, presumably helping to reduce the effect of the reversed conditions at the back of each wave. It is not known whether the physiological differences involved in initiating aggregation persist and play any part in pacemaking.

The strength of a relayed wave at any point depends presumably on the responsiveness of the cells locally, and also on the stimulus they receive, and so on the strength of the wave since its inception. Two opposed waves able to command about equal responses should bar each other's way; but quite a small difference in their strengths at the site of collision might ensure the survival of one of them. If a new wave started from a center before that from a neighboring one, it might be able to exploit a purely temporal advantage and, if they had effectively recovered, reorient the cells beyond the former aggregation boundary. As soon as a gap developed between adjacent organizations, there would be no further possibility of their interaction, had it existed. Examination of Arndt's film of *D. mucoroides*

does show that in early aggregation a wave may invade an area previously conquered from another direction and that waves may or may not cancel on collision.

A ring may form at the forward end of an isolated length of stream if the cells in the lead are attracted back to one side by the cells behind (Shaffer (1956c). On the other hand, a circularly polarized organization sometimes develops while the cells are still separate from one another (Raper 1941). This may arise if a wave is weakened in some area of critical size, or is blocked completely, but is able to cross it in the opposite direction, after spreading round it, as a result of a local increase in strength or a change in responsiveness of the cells within the area, provided that the wave reaches the side it first approached, and so completes the vortex, after the cells there have become ready to respond again and before a new wave (if there was to be one) has arrived. Whether the wave continues to circulate or not, the cells will then have to pursue ever-receding pursuers.

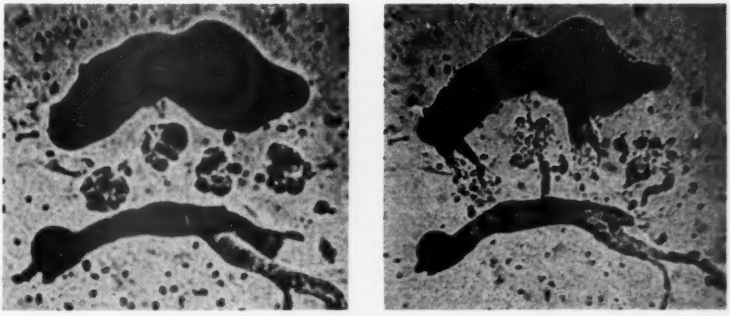
It may be mentioned that in addition to the waves we have been considering, of which at most one or two travel across an aggregation at the same time, there may be very much finer ones. These 'ripples' on the streams, only a few amoeba-lengths between their crests, are revealed most beautifully by Arndt's film. As far as one can see, unlike those of the first kind, they do not cross gaps between cells, and there is at the moment no reason to suppose that they are caused by rhythms of acrasin secretion; perhaps they are of mechanical origin.

SPECIES SPECIFICITY

Raper and Thom (1941) found that mixed amoebae of any two of the species *D. discoideum, D. mucoroides,* and *D. purpureum* would enter joint aggregations, whereas any of these Dictyostelia would form aggregations that were distinct from those made by *Polysphondylium violaceum* in the same area, the streams even overlapping. They further observed that common aggregates of *D. discoideum* and *D. purpureum,* whether arising naturally or as a result of manipulation, would always in time separate into their components, unless they were rushed into building fruiting bodies before they had been able to do so. In contrast, those of *D. discoideum* and *P. violaceum* would not associate even temporarily when placed in contact.

One factor involved is the degree to which the cell surfaces of the different species resemble each other. We may explain the results with the mixed Dictyostelia by supposing that the cells of these species are oriented by the same chemical gradient and that their surfaces are sufficiently similar for them to enter common streams and to be subject to the same flow guidance but different enough for them slowly to sort themselves out. Is it possible to account for the development of the *Dictyostelium-Polysphondylium* mixtures mentioned, simply on the basis of greater differences in their cell-surfaces, without invoking two types of acrasin? Certainly the amoebae of *P. pallidum* can be attracted to a *D. minutum* stream, for which they have such little contact affinity that they are not guided by it

on their arrival but are left to wander about by themselves, sticking to those of their own kind when they meet and eventually forming a stream. This remains applied to the side of the *minutum* stream because of the transverse acrasin gradient it experiences; but possibly it might be attracted away from its bound companion and enabled to join up with another of its own species, if there were a similar pair of streams running close by that temporarily or permanently secreted acrasin at a higher concentration. Whether or not joining up occurs in this way, specific aggregations clearly can be produced using only one acrasin.



A B

FIGURE 3. A. A young fruiting body of *Polysphondylium violaceum* (top) has been laid on the agar parallel to a stream of this species, and four heaps of amoebae, taken from aggregations, deposited between them. The first and third from the right are of *violaceum* also: they start rather nearer the fruiting body but move towards the stream (B). The other two heaps are of *Dictyostelium mucoroides*: they start rather nearer the stream out are attracted to the fruiting body. × 35.

But to return to the mixtures used by Raper and Thom—the amoebae of their Dictyostelia when deposited beside a *P. violaceum* stream are not attracted towards it, though they are to one another's streams. It looks as if here there must be two acrasins involved. A further complication is that these Dictyostelia do respond to young fruiting bodies of *P. violaceum* and even to its older centers and to certain parts of its streams that have begun to develop like centres, whereas these masses often have very much less influence over sensitive amoebae of their own species than do the streams. The simplest explanation of this in terms of specific chemicals is that the *violaceum* streams and young centres secrete an acrasin that attracts *violaceum* amoebae, but that the older stages partially or completely switch over to making the acrasin that attracts certain Dictyostelium species (Fig. 3; Shaffer 1953).

There is, however, a very different explanation available, and though some findings make it an improbable one in the present instance, it does

show the possible refinements of a chemotactic system. Theoretically, two types of amoebae could sort themselves out using only one chemical, if they differed sufficiently in their responses. As an extreme example, if one type reacted rather slowly to an acrasin stimulus and adapted (or fatigued) very little, it would maintain the orientation and secretion induced by the spread of the relay initially. If the other one both reacted and adapted very quickly, a field of its cells could transmit a series of frequent short acrasin pulses, which would control *its* orientation. The two types would be able to form independent aggregations in the same area, provided that their surfaces were sufficiently different for them not to interfere with each other's movements on contact and that the peaks of acrasin concentration produced by the second type were higher than the level maintained by the first. Some separation would still be possible with two types of cells whose behavioral responses were much more alike; but the smaller the differences, the less efficient it would be.

To explain some of the results obtained with different *P. violaceum* sources, one might suppose the pattern of the acrasin secretion of the young centres and streams to be such as to excite the response of *violaceum* amoebae and that of the older centers to be increasingly effective on the amoebae of certain Dictyostelia. There is, though, some evidence obtained from *D. discoideum*, the species most studied, that the frequency of pulses is not critical for orienting the cells used experimentally as 'sensitive'. But the cells in an early stippled aggregation may be more exacting. The inadequacy of the acrasin signal provided by an aggregated mass crawling over them possibly may lie not in the magnitude of a static relative concentration gradient, as was suggested before, but in the absence of an appropriate fluctuation. And though pulses crossing gaps between cells are not visible in some films of mine that record the response of mixed populations to specific gradients, it is just conceivable that waves of acrasin secretion might not affect speed.

Whether any of these specificities, and others discovered by examining further species, *are* due to patterns of secretion and response is thus unknown, and cannot be determined by seeing which cells are attracted to which natural sources. The agar-block test should be more useful, when used with purified acrasins, as it enables us to expose the cells to gradient fluctuations of known frequency. Perhaps the problem should be left till the acrasins produced by different species and different stages have been compared as spots on a chromatogram; and then it can be seen whether there is any residual specificity that cannot be ascribed to chemical differences.

THE NERVOUS SYSTEM

It may not be impertinent to point out that a slime-mould amoeba and a developing nerve fibre are faced with much the same problems in reaching a distant goal; and there are considerable similarities in the way they solve them, even though much recent work (e.g. Weiss and Taylor 1944) has

not supported the view that the tip of a growing nerve can be guided to a remote tissue by a gradient of a chemical that this hypothetically produces (Ramon y Cajal 1928).

(1) According to Weiss (summarized 1941, 1955) the tips of the nerves (of vertebrates) that grow out first are guided by contact with structures in their environment, and especially linear fibrils and microfibrils. (2) As different types of pioneering fibers may choose different pathways when presented with alternatives (e.g. Taylor 1944), this initial guidance must be to some extent selective. (3) The way in which the nerve supply is adjusted to the needs of the area innervated is undoubtedly complex (Hamburger and Levi-Montalcini 1950); but it is clear that the pioneering fibers must convey some information; and it has been suggested that the metabolism of a cell-body changes when its fiber has established connection with its end-organ, and that this, perhaps as a result of the release or absorption of diffusible substances, influences the differentiation of neighboring cell-bodies. (4) A pioneering fiber that happens on its appropriate end-organ becomes adhesive for other nerve fibers, and so (5) is able to guide those growing out from its neighbor neurones to their destination, if they apply themselves to it. (6) These further neurones influence the differentiation of the cells next to them, and their fibers in their turn become adhesive and act as guides. (7) This fasciculation is selective, nerves preferring, to a varying extent, to run beside others of the same type (Oppenheimer 1941; Holtzer 1952). (8) If the end-organ shifts its position, the nerve bundle is towed behind it.

In slime-mould aggregation, as we have seen, (1) the amoebae are first guided by chemical gradients in their environment. (2) These gradients are specific for different species. (3) After the amoebae nearest the center have oriented, and in some cases only after they have made contact with it, they begin to release the chemical and so induce more distant amoebae to start differentiating and to move towards them. (4) The first amoebae to be oriented also become adhesive and so (5) can provide contact guidance for others that apply themselves to them. (6) The more recently recruited amoebae become attractive and adhesive in their turn and both guide those still further away and cause them to differentiate. (7) The formation of streams is selective, amoebae of different species joining preferentially, to a varying degree, with others of their own kind. (8) If the mass at the centre begins to migrate, any streams still flowing into it are towed behind it.

With this degree of similarity in the mechanism or orientation, it is not surprising to find the same patterns developing both in nervous systems and aggregations. Thus, a ring may be formed at the leading end of either a nerve fiber (Wigglesworth 1953) or a stream, if the tip happens to turn backwards; and then round and round the nerve must grow or the cells must flow.

The intercellular connections of the central nervous system, as of an aggregation, emerge in a field of cells that are for the most part unoriented. Because of their inaccessibility and indescribable complexity, it has

proved very much more difficult to determine the factors responsible for their development and orientation than those operating on nerve fibers in the rest of the animal. (Fortunately, an aggregation, on a culture plate, is effectively two-dimensional and displays itself for convenient observation.) The minutiae of the pattern of mutual relationships vary from one individual's nervous system to another's (Lashley and Clark 1946) and from aggregation to aggregation and are doubtless without functional significance. All the variant patterns established by a population of cells, with properties and initial distribution defined within certain limits, will belong to one family; and what we should aim to describe is the Highest Common Form and Function its members will share.

There are some resemblances between an aggregation and a *functioning* nervous system; but as so little is understood about the relevant phenomena is slime moulds, it is difficult to assess the usefulness of making the comparison. For example, self-propagating activities of various kinds can spread along a line of amoebae at speeds as fast as 1.0 mm a minute, or a hundred or a thousand times slower; and they may fail to pass cell junctions in some places. Again, the production of a circularly polarized organization during the early stages of an aggregation is rather similar to the establishment of a wave of contraction circulating round a ring cut out of a jellyfish medusa, which, as Bozler (1926) showed, can be started by blocking one of the pair of nerve impulses that travel in opposite directions round the ring from a common point of origin; though, as the amoebae do not give an all-or-none response, with them there is perhaps only a local weakening or strengthening of one arm of the wave, which would correspond more to Mayer's (1906) original explanation of the jellyfish behavior. As changes in the cell surface are central to them, it is not improbable that these activities of slime moulds and the specificities for which some of them possibly are responsible, could usefully be studied by measuring electrical properties.

SUMMARY

The movement of slime-mould amoebae towards certain collecting centers, which have been started by a few of the amoebae, depends basically on their orientation to the maximum gradient of a chemical, acrasin. Because the gradient is produced by diffusion, the direct range of a center must be limited by the size and maximum sensitivity of the responding amoebae, the amount of chemical that can practicably be produced, and the time needed for orientation to occur after secretion has begun. In fact, its range is rapidly and economically extended by a relay system, as acrasin not only orients an amoeba but induces it to become sticky and secrete acrasin. But as a result, there may be a hundred-thousand sources within an aggregation; and the organism meets the problem of maintaining detectable gradients by inactivating secreted acrasin with an extracellular protein. However, this further reduces the importance of any influence the

chemical secreted by the centre could have at the periphery. The amoebae move towards the center not because of a sustained gradient of secretion outwards from it, but because of the time sequence in which the relay operates. In one type of aggregation, the delay before an oriented amoeba begins to secrete is sufficient for it first to reach the amoebae that attracted it; and as it can then depend on contact guidance, it is not disturbed by the acrasin production of the amoebae on its flanks and at its rear. The result is that the amoebae, stuck together in radial streams, converge on the point where acrasin secretion began. In another type of aggregation, the delay is less, and the amoebae start to make acrasin before they reach their primary attractors; nevertheless, they too condense into radial streams, because, once the field has been polarized, there is a greater probability that an amoeba will continue to be attracted in the direction in which it has been oriented than in any other. The center owes its position not to constantly secreting more than the peripheral amoebae but to secreting before them; and this is primarily due to the ability of its initiator to release acrasin into the medium without their being any there already. If the time relationships of the relay are seriously disturbed, aggregation becomes chaotic. The secretion of a center may fluctuate, and this may lead to the periodic re-excitation of the relay system. The resultant pulses spreading out over an aggregation may reinforce flow guidance in its streams and are especially useful in repetitively reasserting the authority of the center in an aggregation in which the oriented amoebae are not in contact. Also, acrasin is used more economically if an adequate gradient is maintained for only a fraction of the total time. Various reactions with neighboring relay systems are possible: and peculiarities in the spread of a relay may lead to an aggregation's being circularly polarized. Specificity in aggregation may depend on differences in cellular adhesiveness, the acrasin, or the pulse pattern. There are many resemblances between the orientation of aggregating amoebae and of growing nerve fibers.

LITERATURE CITED

Arndt, A., 1929, Die Entwicklung von *Dictyostelium mucoroides*. Institute of Hygiene, University of Rostock. (A film)

1937, Untersuchungen über *Dictyostelium mucoroides* Brefeld. Roux Arch. EntwMech. Organ. 136: 681–747.

Bonner, J. T., 1944a, A descriptive study of the development of the slime mold *Dictyostelium discoideum*. Am. J. Bot. 31: 175–82.

1944b, Fruiting in *Dictyostelium*. Harvard University. (A film)

1947, Evidence for the formation of cell aggregates by chemotaxis in the development of the slime mold *Dictyostelium discoideum* J. Exp. Zool. 106: 1–26.

1949, The demonstration of acrasin in the later stages of the slime mold *Dictyostelium discoideum*. J. Exp. Zool. 110: 259–72.

1950, Observations on polarity in the slime mold *Dictyostelium discoideum*. Biol. Bull. 99: 143–51.

Bozler, E., 1926, Sinnes- und Nervenphysiologische Untersuchungen an Scyphomedusen. Ztschr. vergl. Physiol. 4: 37–80.

Cooke, A. H., Elvidge, J. A. and Heilbron, I., 1948, Fertilization, including chemotactic phenomena in the Fucaceae. Proc. Roy. Soc. London. B. 135: 293–301.

Dethier, V., 1947, Chemical insect attractants and repellents. 289 pp. Blakiston, Philadelphia.

Fraenkel, G. S. and Gunn, D. J., 1940, The orientation of animals. 352 pp. Clarendon Press. Oxford.

Frey-Wyssling, A., 1953, Submicroscoptic morphology of protoplasm and its derivatives. 411 pp. Elsevier, New York.

Hamburger, V. and Levi-Montalcini, R., 1950, Some aspects of neuroembryology; in Genetic Neurology, ed. P. Weiss. 128–60. University of Chicago Press, Chicago.

Holtzer, H., 1952, Reconstitution of the urodele spinal cord following unilateral ablation. II. Regeneration of the longitudinal tracts and ectoptic synaptic unions of Mauthner's fiber. J. Exp. Zool. 117: 523–58.

Lashley, K. S. and Clark, G., 1946, The cytoarchitecture of the cerebral cortex of Ateles: a critical examination of architectonic studies. J. Comp. Neurol. 85: 223–305.

Mayer, A. G., 1906, Rhythmical pulsation in Scyphomedusae. Carnegie Inst. Wash., Publ. 47: 1–62.

Olive, E. W., 1902, Monograph of the Acrasieae. Proc. Boston Soc. Nat. Hist. 30: 451–513.

Oppenheimer, J. M., 1941, The anatomical relationships of abnormally located Mauthner's cells in Fundulus embryos. J. Comp. Neur. 74: 131–67.

Pfeffer, W., 1884, Locomotorische Richtungsbewegungen durch chemische Reize. Unter. Bot. Inst. Tübingen 1: 364–482

Potts, G., 1902, Zur Physiologie des *Dictyostelium mucoroides*. Flora, Jena, 91: 281–347.

Ramon y Cajal, S., 1928, Degeneration and regeneration of the nervous system. Oxford University Press, Humphrey Milford, London.

Raper, K. B., 1940a, The communal nature of the fruting process in the Acrasieae. Amer. J. Bot. 27: 436–48.

1940b, Pseudoplasmodium formation and organization in *Dictyostelium discoideum*. J. Elisha Mitchell Sci. Soc. 56: 241–82.

1941, Developmental patterns in simple slime molds. Growth (Suppl.) 5: 41–76.

Raper, K. B. & Thom, C., 1941, Interspecific mixtures in the Dictyosteliaceae. Amer. J. Bot. 28 : 69–78.

Shaffer, B. M., 1953, Aggregation in cellular slime moulds: *in vitro* isolation of acrasin. Nature, London 171: 975.

1956a, Acrasin, the chemotactic agent in cellular slime moulds. In press. J. Exp. Biol.

1956b, Properties of slime-mould amoebae of significance for aggregation. In press. Quart. J. Micr. Sci.

1956c, Variability of behaviour of aggregating cellular slime moulds. In press. Quart J. Micr. Sci.

1956d, Integration in aggregating cellular slime moulds. In press. Quart. J. Micr. Sci.

Spenser, E., 1590, The Faerie Queene. Bk. 2, Conto XII. W. Ponsonbie, London.

Sussman, M., 1954, The developmental physiology of the amoeboid slime molds; in Biochemistry and Physiology of Protozoa 2: 201–223.

Taylor, A. C., 1944, Selectivity of nerve fibres from the dorsal and ventral roots in the development of the frog limb. J. Exp. Zool. 96: 159–85.

Weiss, P., 1941, Nerve patterns: the mechanics of nerve growth. Growth (suppl.) 5: 163–203.

1947, The problem of specificity in growth and development. Yale J. Biol. & Med. 19: 235–78.

1955, Nervous system (Neurogenesis); in Analysis of Development, ed. B. H. Willier, P. Weiss, V. Hamburger. 346–401. Saunders, Philadelphia.

Weiss, P., and Taylor, A. C., 1944, Further experimental evidence against "neurotropism" in nerve regeneration. J. Exp. Zool. 95 : 223–57.

Wigglesworth, V. B., 1948, The role of the cell in determination. Symp. Soc. Exp. Biol. 2 : 1–16.

1953, The origin of sensory nerves in an insect, *Rhodnius prolixus* Quart. J. Micr. Sci. 93–112.

Wilson, C. M., 1952, Sexuality in the Acrasiales. Proc. Nat. Acad. Sci. Wash. 38: 659–62.

1953, Cytological study of the life cycle of *Dictyostelium.* Am. J. Bot. 40: 714–18.

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TWO DIRECTION EXPERIMENTS WITH HOMING PIGEONS AND THEIR BEARING ON THE PROBLEM OF GOAL ORIENTATION[1]

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INTRODUCTION

We demonstrated in our first experiments with homing pigeons that they can acquire training in a specific direction (Kramer and St. Paul, 1950). We ran two series of trials, imitating on a small scale but under strictly controlled conditions the practice of homing pigeon fanciers of making releases at increasing distances from points on a straight line. After several releases the birds made a beeline for home even if there was a sizable stretch of unfamiliar territory between the new point of release and the preceding ones.

It was fairly evident to us at the time, however, that experiments of this nature did not exhaust the problem of goal orientation. Wild birds can home quickly to their nests without any such directional training. Fanciers reported that homing pigeons will quickly fly back to their old loft when sold or given to persons in distant localities, even if they have had no opportunity to gain flying experience from that direction. Our next step, therefore, was to organize in the summer of 1951 a long-distance release with homing pigeons which had had no preliminary training in direction. The pigeons were released from the top of Gleiberg Castle in the vicinity of Giessen, 200 miles south of their home loft (Kramer and St. Paul, 1952). It was interesting to note that all of the eight groups released separately departed without hesitation toward the north regardless of the direction in which the crates were facing. As there was rising ground north of the point of release, there was nothing that we could see to induce the birds to fly north other than true orientation toward the goal. Homing success was striking, the fastest pigeons arriving home early in the afternoon only 5½ hours after their release. Thirty-two out of a total of forty-seven homed before nightfall and only six in all failed to return.

Since then we have released a large number of pigeons at greater distances and have learned thereby that our choice of a southern point for our first release was a lucky one, for we discovered that the pigeons invariably homed better from the south than from the northeast or east. We were able to make a more thorough study of directional effects in the Durham, North Carolina, area than was possible in Wihelmshaven because the topograph-

[1]The American work covered in this report was conducted under a contract between the Office of Naval Research and Duke University, Nr. 160 244. The German work was part of the research program of the Max Planck-Institut für Meeresbiologie, Wilhelmshaven. Additional funds were supplied by the Deutsche Forschungsgemeinschaft.

ical conditions are more homogeneous there (Kramer, Pratt, and St. Paul, 1956). In the Durham area the pigeons homed best from the south and worst from the north. Homing success from east and west was fair. These results did not fully agree with our Wilhelmshaven experience, for in Wilhelmshaven homing success from Helgoland north of us was good. First reports received from L. Graue in Sacramento, Cal. inform us that homing success in that area seems to be better from the north than from the south, the results from the latter direction being very poor. No physiographical reason has been found there for this phenomenon.

There is no doubt that the pigeons home by virtue of an ability for orientation and not by searching, even in cases where they are released from an unfavorable direction. The physical clues the pigeons use either to get or to maintain their bearings in flight are apparently scarcer when they are flying in certain directions, or else the homing tendency is sometimes overpowered by a directional preference extraneous to the goal orientation mechanism. There is also evidence that homing pigeons can orient themselves better on some days than on others, for in the Carolinas flight results varied from day to day. In Wilhelmshaven (53°N), furthermore, results vary according to the season. Homing times are poor in the winter, even in good weather, and losses are high even at distances as short as 14 miles (Kramer, 1954; Kramer and St. Paul, 1956). In Durham, North Carolina (33°N), this seasonal effect has not been observed and flight results can be good as well as bad in cold weather. Few summer flights have been made there, however, and the comparison may be complicated excessive temperatures.

TWO-DIRECTION RELEASES WITH PIGEONS OF CONSANGUINEOUS STOCK

The discovery of the directional effect and its bearing upon the all-round ability of pigeons to orient themselves made it necessary to reconsider the results of the Gleiberg Castle releases. To check upon our interpretation of the earlier results, we needed to make two-direction releases from the same spot; that is to say, to the south as well as to Wilhelmshaven. Therefore, we decided to establish a loft in Freiburg, 185 miles south of Gleiberg Castle, and the first pigeons were sent there from Wilhelmshaven in the fall of 1952 to form the nucleus of the new colony. Under the care of Frau Gertrud Geinitz the loft multiplied rapidly and furnished 29 pigeons for the first joint release in August, 1955.

The pigeons for this release, conducted by U. V. St. Paul, were shipped by rail from Freiburg and Wilhelmshaven during the night of August 1st. They were picked up at Giessen station the next morning and taken to Gleiberg (3 miles along the road) in a closed van which admitted no day-light. After a 24-hour rest under the open sky 5 pigeons were released on the morning of August 3rd when the sky was overcast. The flight results of this release will be given at the end of the report on the August 4 results. Although the sky was partly cloudy on August 4th and it was necessary to interrupt proceedings while a bank of clouds swept past the sun, it was possible to release all the other birds before noon in bright sunshine. Wilhelmshaven and

Freiburg pigeons were released atlernately. All 15 Wilhelmshaven birds were released singly, but 14 out of the 27 Freiburg birds were released in pairs as contrast conditions to the south were too poor for single birds to be followed long enough with field glasses.

The results are given in Fig. 1. The vanishing diagram of August 4 (lower part, outer circle) displayed a well-defined separation between the direction of flight of the Wilhelmshaven and Freiburg birds. It was reported,

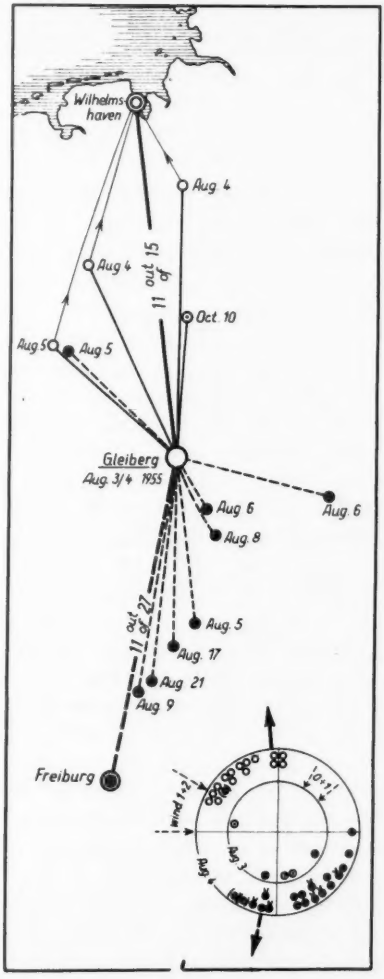

FIGURE 1. Initial flight directions (bottom to the right) and recoveries of pigeons released from Burg Gleiberg to Wilhelmshaven (200 miles north) and to Freiburg (185 miles south). Open circles refer to Wilhelmshaven colony, black circles to Freiburg colony. Circles with dot at center indicate pigeons released on August 3, plain circles such released on August 4.

furthermore, that in the great majority of cases the pigeons flew off without hesitation or circling.

Homing success varied considerably. However, the Wilhelmshaven pigeons did much better than the Freiburg birds (Table 1), particularly when it is considered that 14 of the latter were released in pairs. Pigeons released in groups have a better expectation of success than singletons. (See also Hitchock 1955).

TABLE I

HOMING RESULTS OF THE AUGUST 4, 1955, GLEIBERG CASTLE RELEASE

Date of Arrival:	Aug. 4	Aug. 5	Aug. 6–16	Lost	Total
Wilhelmshaven	3	8	3	1	15
Freiburg	3	5	3	16	27

It is only possible to conjecture as to the reason or reasons for the poor homing success of the Freiburg pigeons. From a purely mechanical standpoint, the southern course was easier rather than more difficult, for it was slightly shorter (185 mi. as against 200 mi.) and was favoured by a slight breeze blowing out of the northern semicircle. It was ascertained that the weather conditions were not such as to create a more advantageous situation for the north homers. The two lofts had had different flying experience, however. The Freiburg pigeons had made three to six flights of nine to twenty-two miles from all around the compass. In addition, two of them had flown fifty-six miles the year before from a southerly direction. Four of the Wilhelmshaven pigeons, on the other hand, had made flights of up to forty miles from easterly and westerly directions. The other eleven had made in addition a flight of fifty-nine miles from south to north, but this long flight had been the preceding one in only one case. Although the Wilhelmshaven pigeons had more flying experience behind them, their better homing success cannot be attributed to this fact alone, for all other releases have shown that Wilhelmshaven pigeons home easily from Giessen. For example, on July 24 and 25, 1953, A. and K. Rawson released in Giessen 24 young Wilhelmshaven pigeons which had only made two or, at the most three, flights not exceeding fourteen miles. Fourteen of these young pigeons arrived home the day they were released, three the next day, four later, and only three were lost. One of the late arrivals was an inexperienced pigeon taken to Giessen by mistake. It had done no flying at all except around the loft.

The poor homing success of the Freiburg pigeons is probably connected with what we call the directional effect in orientation. This is indicated by both the wider spread of the southern vanishing diagram and the very wide scattering of Freiburg reports (Fig. 1). We have released roughly 200 Wilhelmshaven pigeons in Giessen, most of them in groups, and not one of them was found so far out of its way as two of the Freiburg pigeons.[2] While the

[2] Attention may be called also to the fact that the report dates of the Freiburg birds range significantly later than those of the Wilhelmshaven birds at comparable distance, which is much in harmony with the number of birds homed to either place.

question of the different accuracy of orientation towards the south and towards the north is a matter requiring further investigation before it can be cleared up, it is certain that the Wilhelmshaven vanishing directions and reports are widely divergent from those of Freiburg.

A few words remain to be said about the five pigeons released on August 3rd when the sky was completely covered by a thin blanket of clouds. The flight behavior of the pigeons on release confirmed long experience to the effect that pigeons are not well oriented when they fly off under such circumstances. The vanishing observation of these five birds (fig 1, inner circle) are not strictly comparable to the ones released on August 4, because they all lingered longer in the vicinity of the tower and this fact alone would tend to produce more widely scattered vanishing points. No noticeable difference in homing success in comparison with a good-weather release is to be expected over such a distance, particularly not with such a small number of birds. One of the two Freiburg pigeons released on August 3rd arrived home the same day, but no trace was found of the other. One of the Wilhelmshaven pigeons arrived in 5 to 8 days, another was found on the way, and the third disappeared altogether.

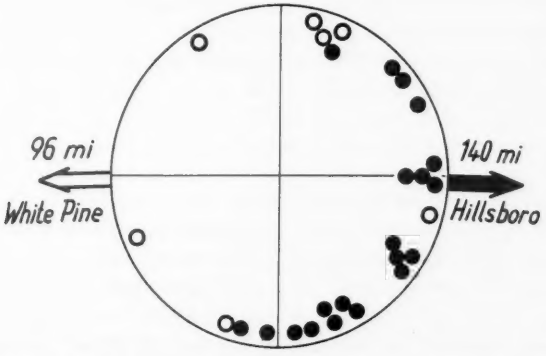

FIGURE 2. Initial directions of pigeons released on Dugger Mt.. Open circles refer to birds from White Pine, Tenn., black circles to such from Hillsboro, N. C..

In the fall of 1953 a number of young pigeons belonging to the Duke University Colony were taken to White Pine, Tennessee, to form a branch colony. Eight of the transplanted birds, aged four to six months, were released for control purposes, with twenty pigeons from the Hillsboro loft of the parent colony, from the fire tower on Dugger Mt. (3333 ft.). The results of this release will only be touched on briefly here, for they were reported by Pratt and Thouless (1955). The Hillsboro pigeons flew off without hesitation in a homeward direction (18 out of 20 vanishing directions were in the home semicircle), but all of the White Pine birds hesitated before taking off and they did a great deal of circling. When they finally flew away, their vanishing directions were randomly distributed around the whole

circle. Homing was poor: 3 out of 8 White Pine birds (96 mi.) homed by the fifth day. One out of the 20 Hillsboro birds (140 mi.) returned after 10 days, and a second one at a later time. One Hillsboro bird was found after traveling one-third the distance toward home.

Pratt and Thoulees also released 3 White Pine birds and 3 Durham birds at Lick Stone firetower, 40 miles south of the Tennessee loft and 238 miles west of Durham. All three White Pine birds vanished in the general direction of home and all were home by the third day. The Durham birds did not show any homeward tendency at the release point, but one homed after several days.

EXPERIMENTS WITH PIGEONS OF DIFFERENT STOCK

The three experiments so far reported have in common one important feature: In each of them the two loft groups were of consanguineous origin. So far, these three releases are the only ones controlled from the genetical side. However at the present stage of the research, it was important to make observations also in situations where no consanguineous material was available.

Another two-direction release reported by Pratt and Thouless was one of this type. Six birds were shipped by railway express from Richmond to Durham and were taken with 25 birds from two Durham lofts to Piney Mt., 101 miles north of Durham and 75 miles west of Richmond. Singleton releases were made until shortly after noon on Sept. 23, 1953 with good weather conditions (clear and mild; wind 8–13 mph N. E.). Of 21 vanishing points of Durham birds recorded, 19 were within the quarter of the circle centering on the home direction, and the other two were toward the east, about 90° off the home line. Only 2 of the 6 Richmond birds vanished toward home while the other 4 started south. These ambiguous results of the small control group did not help in interpreting the homeward departures of the larger Durham group. However, 4 birds of the Richmond group and 7 of the Durham group homed by the day after the release; 4 more Durham birds homed later. These returns indicate that orientation was present in both groups.

A two-direction release was made on April 15, 1954 from Ansonville fire tower with birds from Durham (90 mi., 48°) and Mountville, S. C. (117 mi., 255°). The Durham birds had been transported to Mountville on the preceding day and were brought back to Ansonville with the Mountville birds during the night. The Mountville birds had made two previous homing flights: one of two miles from the west and one of 40 miles from the south. The Durham birds had made several flights from various directions, but in no instance had the immediately preceding flight for any bird been from the south or west sector.

The weather was mild with a slight breeze from the S.W. (2-6- mph) and with a high layer of cirrus clouds through which the sun was always visible. The atmosphere was hazy at the ground level but with good visibility, estimated at 10 miles. The releases were started at 10:00, alternating with single birds from the two lofts. The birds proved to be very hesitant about

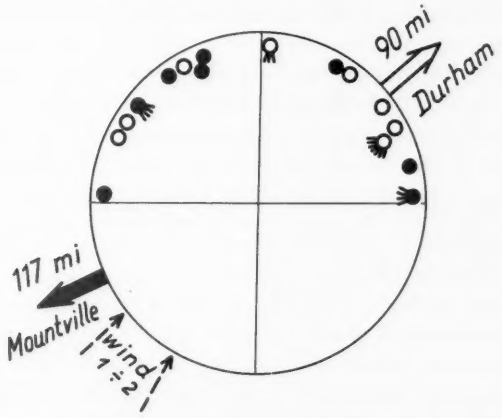

FIGURE 3. Inititial directions of pigeons released from Ansonville, N. C., to Mountville, S. C. (black circles) and to Durham, N. C. (open circles). Bristles at circles indicate number of birds composing groups.

departing on this occasion. Of 12 birds released singly, 5 took more than four minutes to go out of sight, the longest vanishing times being 17 min. The longest vanishing times recorded on a "good" day rarely exceed 4 min. Because of those long vanishing times, it became inevitable to release part of the birds in groups.

The vanishing points (Fig. 3) were all in the northern semicircle, and with no appreciable difference between the birds from the two lofts. 15 out of 16 of the Durham birds homed, ten of them on the release day. None of the Mountville birds returned to the loft.

The first impression given by these results is that there was a general north-going tendency shown by the overall results. In a final section, however, this statement will be reconsidered.

An experiment based upon the principle of two-direction releases, but on a more elaborate plan, was made in October, 1954 with pigeons from Durham, N. C. and Richmond, Va., which are 140 miles apart. Simultaneous releases were made from two towers, each involving birds from both lofts. For the geometrical lay-out, see figure 4. Releases were made on two occasions, Oct. 1 and Oct. 17. This experiment has been described in greater detail by Pratt (1956).

The birds from the two cities were transported after midnight to a point approximately half way between the two lofts. There the birds from each city were divided and reassigned to vehicles going to the two release points. Durham and Richmond birds were released alternately at both places during the forenoon.

For the Richmond birds, this was the first release out of sight of the loft. They showed a distinct choice of the homeward direction at both places and 19 out of 25 birds reached home. About half of the Durham birds had homed

previously from distances of 5-20 miles, the home direction on the immediately preceding flight being different from that provided in this release. A somewhat more vague choice of the home direction at the release point was shown by the Durham birds and only 8 out of a total of 28 returned.

Eighteen Richmond birds and the 8 Durham birds that homed the first day were used again on the second occasion, the release points being reversed. Other Durham birds were added to provide a sufficient number for a full scale release. The departure patterns in the second release on the whole showed a more accurate choice of the home direction. Out of 47 vanishing points recorded, 40 were in the home semicircle. Homing success was slightly higher as well on the second occasion, 15 out of 18 birds reaching Richmond, and 14 out of 30 returning to Durham.

Weather conditions seemed good on both occasions over the entire area, and all releases were made in bright sunshine. No difference was observable between the two days to account for the impressive differences in both departures and homing success.

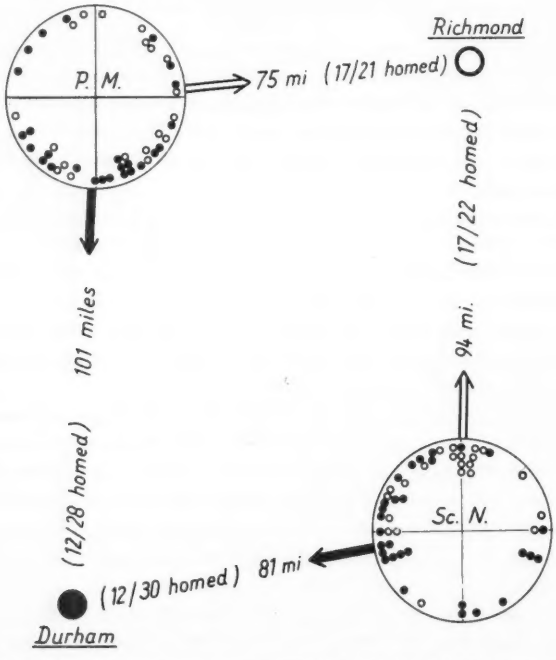

FIGURE 4. Design of "rectangle experiment". Initial flight directions at the two release points (Piny Mount, Scotland Neck) are given. Black dots refer to the Durham loft, open dots to the Richmond loft. Departures from Scotland Neck are more accurate than those from Piny Mount. However, only in one group (Piny Mount to Richmond) the preponderance of departures in the homeward half-circle is not statistically significant. By comparing all homeward departures to all opposite departures a high statistical significance of the overall homeward tendency is obtained: $\chi^2 = 25$ with 1 d. f.

The superiority in homing success shown by the Richmond birds is statistically reliable. The conditions of the experiment do not permit a clear-cut interpretation of this finding, but it appears likely that both the directional effect and stock differences may have contributed to this difference.

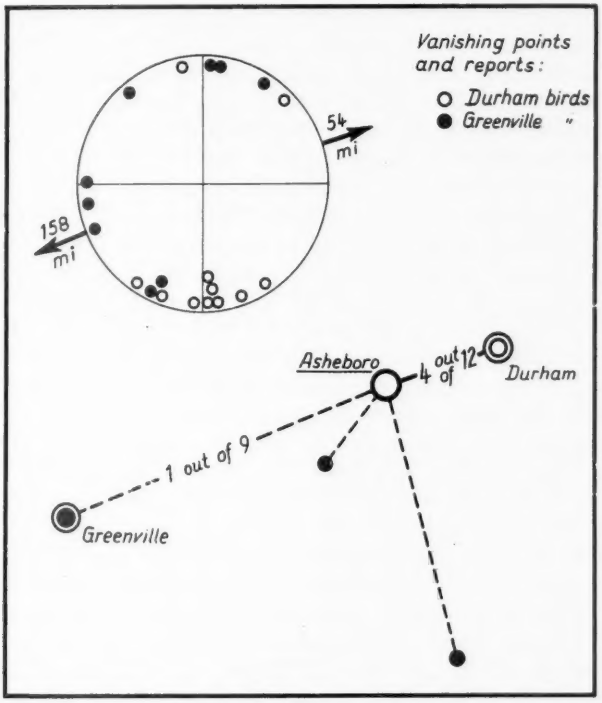

FIGURE 5. Asheboro release: Vanishing diagram (upper part) and map with two reports.

On Dec. 4, 1954, a two-direction release was made at Asheboro, N. C., with nine birds from Greenville, S. C., 158 miles S. W., and 12 birds from Durham, 54 miles N. E. This was the first release for both groups. The Greenville birds gave some indication of homing orientation at the release point (fig. 5), but the Durham birds showed an orientation toward the south, nine of eleven vanishing points being closely grouped about this point. This effect was possibly due to the fact that the city of Asheboro was situated about a mile away in that direction. Birds of the Durham loft had been observed previously to be drawn toward a strange city in a direction away from home (Pratt and Thouless, 1955). Homing success was unusually poor, only one bird returning to Greenville and 4 to Durham. One Greenville bird was reported about a third of the way toward home, and a second was found at a distance of 125 mi. about 90° off the home course.

DISCUSSION

In those U.S.A. areas to which our knowledge extends, orientation towards goals is less clearly demonstrable than in England (Matthews, 1955) and Northern Germany. This depends partly on the circumstance that few reports of birds found on their way are obtained in America. Nevertheless, there is a general impression that orientation is actually more or less easy to observe here than in Europe. In his release in the Ithaca, N. Y. area, D. R. Griffin (1952) observed orientation which he attributed to landmarks. H. B. Hitchcock's (1956) observations in Vermont show very poor initial orientation and homing success, although they make it difficult to believe that sheer random orientation is at work. In the Durham area initial orientation is missing or paradoxical, i.e., the departures point to directions other than home in more cases than in Germany and particularly in England. H. L. Yeagley's (1951) pigeons gave widely scattering report patterns, but still gave evidence of a homeward tendency in some cases. Recently, D. R. Griffin released 29 pigeons of one of the Duke University loft groups (Hillsboro) on three occasions at a distance of approximately 600 miles to the N. E. We wish to express our thanks to Dr. D. R. Griffin for allowing us to mention his observations. In one release, all eight birds headed in the general direction of home, but the other two releases (one of them at the same place) gave randomly-distributed vanishing points. It is not possible to interpret the one "good" release as a proof of genuine homeward orientation since no homing success or reports on the way give any indication of goal-directed locomotion. It is true that in Northern Germany releases from the east and north-east always give poorer results in initial orientation and homing success than from other directions; yet at a distance of 100 miles even there initial orientation is clearcut and reports show that the initial direction was really "meant." So there seems to be an overall difference in orientation accuracy between the two areas. One would be inclined to think such a difference is caused by genetical differences of the pigeon breeds, and indeed exchange of stock remains a requirement of high priority in any case of differential results. But it is difficult to explain the whole story by differences of breed, because there seem to be also marked differences of orientation accuracy within the southeastern part of the U.S.A. While it is hopeless to interpret the observations represented by Fig. 4 on the assumption of random searching, the Ansonville release did not indicate a relation of the observed flight directions to the two goals. The conclusion based on this release by itself would be a one-direction orientation which happened to lead the pigeons toward Durham. However, considering the whole complex of observations, such a conclusion does not recommend itself. Absence of evidence of orientation does not prove absence of orientation. As we have seen in the Gleiberg two-direction release, and as has been explained in a paper particularly devoted to the direction effect (Kramer, Pratt, and St. Paul, 1956), we must expect differences in orientation with reference to the flight directions. In the Ansonville case those differences may just be strongly pronounced.

In addition to the evidence pointing to regional differences in orientation, that is, more accurate departure patterns in Germany and England than in Eastern U.S.A., and to differences related to flight direction, there is also evidence that homing pigeons can orient themselves better on some days than on others, for in the Carolinas flight results varied from day to day. The differential results in the two rectangle releases were suggestive in this sense. The Ansonville release is open to an interpretation of this sort; no other releases from Ansonville were made.

Within any particular region, therefore, repeated releases to the same loft from a given point are required to show definitely whether poor results are attributable to factors of location or to variations in these from time to time. However, there is already a strong indication that regional differences do exist. In additional to the evidence submitted in this paper, it may be remembered that H. L. Yeagley's (1947) hypothetical explanation of the homing ability of pigeons was inspired by a statement which seemed to be generally accepted among pigeon fanciers: Pigeon races in the state of Indiana give poor results. It may also be argued that the well-established direction effect is but one particular aspect of the phenomenon of regional differences.

SUMMARY

In seven cases birds from two different lofts have been released at intermediate points. In two cases (Giessen; rectangle release) the birds showed clearcut orientation to the two goals. The evidence comes from the initial heading directions as observable by field glasses from the release points; from achieved homing; and in the case of the Giessen releases, from birds reported on their way. In four other cases (Piney Mt., Dugger Mt.; Lick Stone; Hillsboro) there was differential behavior of the members of either colony; however, without obvious orientation toward both goals. In one case (Ansonville) the behavior of all birds at the release was equally undecided; vanishing directions could not be differentiated; homing success was achieved only by those pigeons whose home was situated N. E. (Durham).

In the case of the Giessen, Dugger Mt., and Lick Stone releases, the two colonies were of consanguineous origin. In the rest of the releases the stocks were of different breed.

The cases in which only ambiguous or no true goal orientation at all can be recognized require a special explanation. It is thought that regional differences may exist in the physical substrate which provides orientation clues. Regional differences of this sort may be connected with, or represent another aspect of the directional differences in homing.

REFERENCES CITED

Griffin, D. R., 1952, Aeroplane observations of homing pigeons, Bull. Mus. Comp. Anat., 107: 411-440.

Hitchcock, H. B., 1955, Homing flights and orientation of pigeons, Auk. 72: 355-373.

Kramer, G., 1955, Einfluss von Temperatur und Erfahrung auf das Heimfindevermögen von Brieftauben, J. Orn., 95: 343-347.

Kramer, G., Pratt, J. G., and St. Paul, U. V., 1956, Directional differences in pigeon-homing, Science, 123: 329-330.

Kramer, G., and St. Paul, U. V., 1950, Ein wesentlicher Bestandteil der Orientierung der Reisetaube: Die Richtungsdressur, Z. Tierpsychol., 7: 620-631.

1952, Heimkehrleistungen von Brieftauben ohne Richtungsdressur, Verh. dtsch. Zool. Ges., 1951, 172-178.

1956, Weitere Erfahrungen über den "Wintereffekt" beim Heimfindevermögen von Brieftauben. (In press).

Matthews, G. V. T., Bird navigation, 1955, Cambridge University Press.

Pratt, J. G., 1956, Testing for an ESP factor in pigeon homing: requirements, efforts, and difficulties. Ciba Foundation Symposium on Extrasensory Perception. Boston: Little, Brown.

Pratt, J. G., and Thouless, R. H., 1955, Homing orientation in pigeons in relation to opportunity to observe the sun before release, J. Exp. Biol., 32: 140-157.

Yeagley, H. L., 1947, A preliminary study of a physical basis of bird navigation, J. Appl. Phys., 18: 1035-1064.

1951, A preliminary study of a physical basis of bird navigation, J. Appl. Phys., 22: 746-760.

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DEVELOPMENTAL HOMEOSTASIS OF BODY GROWTH IN MICE*

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In spite of various kinds of variations in the environment which occur during the course of their development, organisms tend to become adjusted so that their tissues, organs, morphology and physiology result in what is commonly considered normal for the species. Waddington (1953) has described this type of buffering mechanism in the development of an organism as "canalization." Indeed, the self-regulating abilities of organisms are of significance in evolutionary theory and animal and plant breeding as well as in development. This phenomenon has been variously described as plasticity (Salisbury 1940), existential adaptation (Goldschmidt 1948), stability (Mather 1953, Jinks and Mather 1955), phenotypic flexibility (Thoday 1953), developmental feedback (Warburton 1955), homeostasis (Dobzhansky and Wallace 1953, goes back to Cannon) and developmental homeostasis (Waddington 1953a, Lerner 1954).

The phenotypic variability of genetically homogeneous populations may be considered as an index of buffering or homeostatic capacity since it measures the magnitude of divergence of individual phenotype from the mean of the population (Lerner 1955). Thus a comparison of such populations in regard to the changing variability of a character during development should reflect the differences in pattern and *capacity* of this property. Most studies of quantitative variation have been made from observations of a trait only at a single stage in the life history of an organism, and thereby have neglected the possible changes taking place in the variability during development. The purpose of the present communication is to examine some data on general body growth at different periods during postnatal development in genetically different groups of mice. The general results bear not only on the nature of gene action on body size but also on differences in developmental homeostasis among genotypes.

MATERIALS AND METHODS

The data for this study were obtained from the F_1, F_2 and first backcross generations from reciprocal crosses between Large and Small strains of mice. Both parental strains were developed by selection for body size in the two directions for many generations and then followed with inbreeding as reported previously (Chai 1956a). Data on litter size, parity and maternal age in each of these groups have been given elsewhere (Chai 1956b).

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TABLE 1

MEANS AND SQUARED COEFFICIENTS OF VARIATION OF BODY SIZE OF MICE FROM DIFFERENT INBRED AND CROSSBRED POPULATIONS AT BIRTH. WEANING AND 60-DAYS OF AGE.

Genotypic groups	Birth			Weaning			60-day		
	No.	Mean (gram)	$(C.V.)^2$	No.	Mean (gram)	$(C.V.)^2$	No.	Mean (gram)	$(C.V.)^2$
P_L	78	1.8	130	48	20.1	108	41	37.4	26
P_S	95	1.2	108	75	9.1	88	65	13.6	23
P_M		1.5	119		14.6	98		25.5	24
F_1	138	1.7	59	162	16.5	47	161	25.8	19
F_2	321	1.5	74	231	18.3	95	216	27.2	113
B_1	275	1.6	68	307	16.5	92	318	26.2	98

Remarks: 1. Crossbred types included:
$S♀ \times L♂$, $L♀ \times S♂$ in F_1
$(S♀ \times L♂)^2$, $(L♀ \times S♂)^2$ in F_2
$S♀ \times (S♀ \times L♂)♂$, $S♀ \times (L♀ \times S♂)♂$, $(S♀ \times L♂)♀ \times S♂$, $(L♀ \times S♂)♀ \times S♂$
$L♀ \times (L♀ \times S♂)♂$, $L♀ \times (S♀ \times L♂)♂$, $(L♀ \times S♂)♀ \times L♂$,
$(S♀ \times L♂)♀ \times L♂$ in B_1

2. $(C.V.)^2 = \left(\frac{S.D.}{Mean} \times 100\right)^2$

The body weight of each mouse was taken at three different stages: birth, weaning (28 days) and 60 days of age. The total number of mice, means and variabilities in terms of squared coefficients of variation $(C.V.)^2$ of body weight were computed for each group (table 1). Since there were sex differences in body weight and differences in sex ratios within each sub-group, the group means were obtained by averaging the means of males and females within each sub-group and averaging again the sub-group means. This procedure might not be rigorously valid for obtaining an unbiased estimate; however an equal weighting was allowed for each sex and should be adequate treatment for present purposes. No corrections were made for differences in litter size, litter seriation and maternal age. The reasons for this omission have been discussed (Chai 1956b).

Since the magnitudes of the standard deviations of body weights were shown to be generally dependent upon the means, the squared coefficient of variation was taken as a basis for comparing variabilities of the different groups. Although there might be some better transformation which could be applied, the present one is not apt to cause serious error (see Reeve and Robertson 1954). The standard deviations used for computing the coefficients of variation were derived from the variances within litters. The latter were obtained by removing the between-litter variation statistically from the total variation.

The removal of the between-litter variation from consideration in these analyses is based on the fact that a portion of the litter variation obtained in this study could be attributed to artificial error and various environmental factors which were distributed disproportionately among the several

groups. For example, since observations for newborn litters were made only once a day, the 24-hour interval permits a considerable error in actual birth weights partly due to rapid growth at this stage and partly due to differences in time of nursing and amount of milk suckled. Additional sources of bias were differences among groups in the age of the parents, litter sizes and litter seriation. Although contributing some error to the estimates of between-litter variation, these influences should not affect the within-litter variation. Therefore, only the within-litter variation has been taken into consideration in this study.

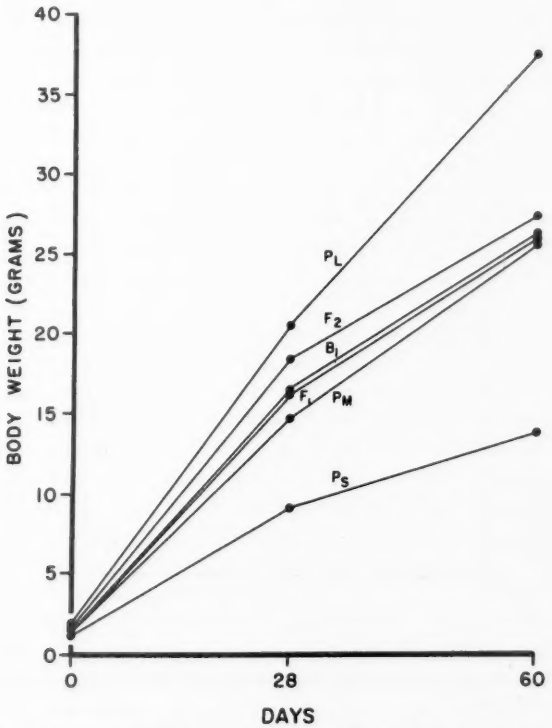

FIGURE 1. Illustrating the differences of body size and rate of growth of mice in the different genotypic groups. Plots were means of body weight at birth, weaning and 60-days of age.

The average body sizes and rates of growth are graphically illustrated in figure 1 based on the means in table 1. The differences between the Large and Small mice are not only in mean body weights but also in rates of growth, especially in the period between weaning and 60-days of age. This indicates that the Small mice probably reached full growth earlier than did the Large mice. This seems to reflect a growth phenomenon common to most organisms. The slightly higher mean values of the F_1 over those of

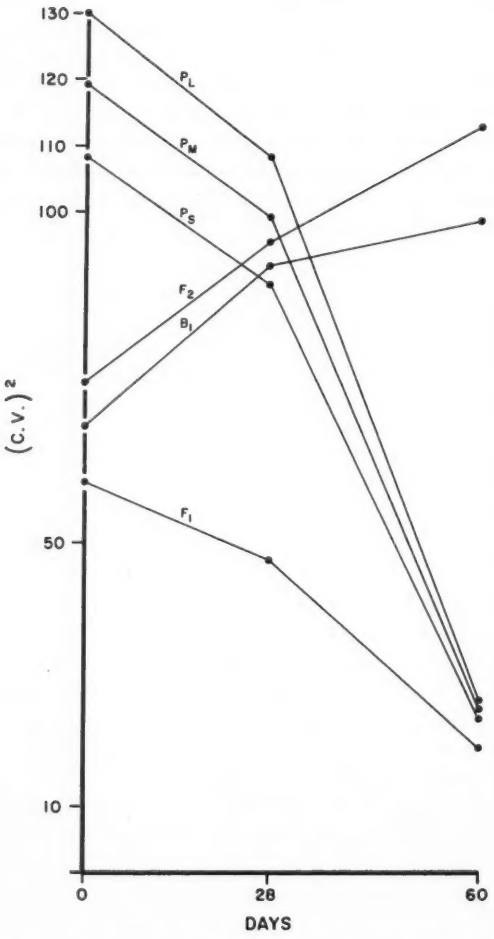

FIGURE 2. Illustrating the differences of variability during growth at birth weaning and 60-days of age within and among different genotypic groups of mice. (for details, see text)

the mid-parent indicate a relatively greater net genetic effect of the Large mice over the Small mice. The higher means of the F_2 progeny as compared with the F_1 was likely due to augmentation of their growth by the maternal influences of the F_1 mothers.

More significant were the differences in variability within the different genotypic groups as expressed by the $(C.V.)^2$ (table 1 and figure 2). During growth the variability decreased within each relatively genetically homogeneous population (P_L, P_S and F_1) while it increased in the genetically heterogeneous populations (F_2 and B_1). The order of magnitude of

$(C.V.)^2$ at each successive time of measurement was $P_L > P_S > F_1$ in the homogeneous groups and was $F_2 > B_1$ in the heterogeneous groups. The over-all picture of both the means and the variabilities requires genetic interpretation.

DISCUSSION

In the study of evolution, considerable attention has been focussed upon the genetic changes of the population subjected to selection. Waddington (1952) has pointed out that the intensity of canalization can be increased by selection. A population long selected for a certain optimum would tend to acquire a stronger buffering or self-regulating ability due to accumulation of a new combination of genes with dominance and epistatic effects. This is in agreement with the ideas suggested by Lerner (1954). If this hypothesis is true, then such stabilizing selection would result in a decreased variability of the trait under selection. The tracing of the breeding histories of the inbred lines of mice in the present study may support this hypothesis. Crosses between two such lines would result in a breakdown of the gene combinations conferring homeostatic properties and the variabilities would be expected to increase. In the case where the selected lines were also inbred, the F_1 hybrid would gain a buffering capacity due to their acquired heterozygosity. Their variability would be expected to remain low.

The differences in the patterns of declining variabilities from weaning to 60 days of age between the parental strains and the F_1 hybrid reflect the basic differences in their abilities. The great differences in their variabilities at birth indicates the more effective buffering mechanism of body growth operating in the F_1 hybrids, at least at the beginning of their prenatal development. It is explainable by their genetic make-up. Since the inbred lines were derived by selection, their self-regulating properties are expected to be based upon specific groups of genes acting approximately at that time of development when body size was used as the criterion of selection. On the other hand, the F_1 hybrid would be expected to possess a buffering capacity which originated in a different manner from that of the parental lines, for example, a property probably resting upon heterozygosity *per se*. This might be expected to be operating throughout the development of the animal.

Without analyzing the variability in the F_2 and backcross generations, the importance of the contrast in results between these and the parental strains and their F_1 hybrid would not be as convincing. Yet these statistical values should not be taken too seriously as nothing is known about the amount of sampling error involved. Considering these values at their face value, however, the general pattern presented by the F_2 and B_1 generations seems to reflect the time of action of genes of the selected loci randomly segregated in individuals of these groups. These mice with different genetic constitutions would tend to develop near to their genetically

determined norms which presumably would be distributed within the range of the means of the Large and Small strains of mice. Thus, along with the growth of the animal, the variability of individuals within these groups increases as these genes assume their role. Concomitantly, the originally endowed self-regulating property resulted from selection of the parental strains would be expected to deteriorate following the disintegration of the specific genic combinations. Thus the variability would increase due to both genetic segregation and the loss of the self-regulating property.

The greater variability in the parental strains than in the F_2 and backcross generations at birth is contrary to expectation. It has been generally believed that a poor environment usually causes greater variation in animals from the same population. The maternal environment of the inbred mothers might be less favorable than that of the F_1 hybrids and contribute thus an additional environmental variation to the newborns of the inbred lines. This can be tested by comparing the variation between the subgroups of animals produced by the inbred mothers and by the F_1 mothers in the backcross generations. It was found however that the average variability of the offspring from the inbred mother is no greater than that of the offspring from the F_1 mothers. It was observed during the experiment that the F_2 newborns produced by the F_1 mothers were vigorous and healthy with fewer stillbirths and generally appeared more uniform in size than the young in any of the other groups. Whatever are the contributory factors, it seems to be that the genetic contribution is relatively small at birth, by the time of weaning the effects of the maternal influence are declining and the effects of specific genes are assuming relatively greater importance. The relative change in magnitude of these two components during development would be interesting to observe and will be studied separately in a future investigation.

SUMMARY

Observations of variability of body size at different periods of postnatal growth of mice from different inbred and crossbred populations have been presented. The variability following body growth was shown to decrease in both inbred and F_1 hybrid groups of mice but to increase in the backcross and F_2 generations. Inferences concerning developmental homeostasis and time of gene action have been made.

LITERATURE CITED

Chai, C. K., 1956a, Analysis of quantitative inheritance of body size in mice. I. Hybridization and maternal influence. Genetics: 41: 157–164.

1956b, Analysis of quantitative inheritance of body size in mice. II. Gene action and segregation. Genetics: 41: 165–178.

Dobzhansky, Th., and B. Wallace, 1953, The genetics of homeostasis in Drosophila. Proc. Nat. Acad. Sci. 39: 162–171.

Goldschmidt, R. B., 1948, Ecotype, ecospecies and macroevolution. Experientia 4: 465–472.

Jinks, J. L., and Mather, K., 1955, Stability in development of heterozygotes and homozygotes. Proc. Roy. Soc. B. 143: 561–578.

Lerner, I. M., 1954, Genetic homeostasis. N. Y. Wiley.

1955, Buffered genotypes and improvement in egg production. Amer. Nat. 89: 29–34.

Mather, K., 1953, Genetic control of stability in development. Heredity 7: 297–336.

Reeve, E. C. R., and F. W. Robertson, Analysis of environmental variability in quantitative inheritance. Nature 171: 874.

Salisbury, E. J., 1940, Ecological aspects of plant taxonomy. New Systematics 329–340.

Thoday, J. M., 1953, Components of fitness. Symp. Soc. Exp. Biol. 7: 96–113.

Waddington, C. H., 1952, Canalization of the development of quantitative characters. Quantitative Inheritance. London. Her Majesty's Stationery Office.

1953, Epigenetics and evolution. Symp. Soc. Exp. Biol. 7: 186–199.

1953a, The "Baldwin Effect" "genetic assimilation" and "homeostasis" Evolution 7: 386–387.

Warburton, F. E., 1955, Feedback in development and its evolutionary significance. The Amer. Nat. 89: 129–140.

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SEX-CHROMOSOME INVERSIONS IN CHIRONOMUS

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Generally, the only guide to the sex of a larva of Chironomus is the structure of its gonads; the giant chromosomes are normally the same in male and female. However, there are occasional exceptions. In *C. tentans* there are two inversions, each in a different chromosome, which are inherited from male to male, and so must be in the Y-chromosomes (Beermann, 1955). These results were obtained using insects from Germany and Sweden. As no larvae were found in which these particular inversions occurred together, and as no homozygotes for either inversion were ever seen, my own observations (Acton 1956) suggest that the same may be true in England. Except perhaps for a population in Sweden, neither of the inversions is found in all males, so that many are not distinguishable from females by their giant chromosomes. In contrast, every male larva of *C. annularius* was found to be heterozygous for a complex inversion (Beermann, 1955); again the samples were from Germany and Sweden.

It is important that the inheritance of these inversions should be determined in larvae from other countries to see whether geographical isolation has allowed the populations to diverge in respect of their sex-chromosomes. I have sexed a total of 105 *C. annularius* larvae from widely separated localities in Britain, and of these 46 were males; with one doubtful exception, all the males were heterozygous for the inversion described by Beermann. One of the 59 females was heterozygous for a different inversion in very much the same part of the chromosome as the one just mentioned, but none of the other females had an inversion in this chromosome. Thus over a wide area all larvae of *C. annularius* which have been sexed have an inversion in the Y-chromosome; as would be expected, neither Beermann nor I have seen homozygotes for this inversion.

I have studied three other species of the subgenus, but two of them are not yet certainly identified; these are *C. cingulatus* and *C. plumosus*. Though I have examined only a few larvae of the former species, these were enough to show that no inversion is found in all males. This point is made because parts of the banding-pattern of the chromosomes seem to be similar to parts in *C. annularius*, and in addition the imagines are almost indistinguishable. As there is a reason for supposing that the two species are closely related, the comparison is of some value.

On the other hand, there is an inversion in *C. plumosus* which I have so far found only in males, and in only one of the three populations studied. The probability that this distribution is random is 3.5×10^{-3} (Fisher's

exact method). The other three inversions in this species were found as frequently in females as in males.

	Chromosome 1	
	Uninverted	Inverted
Male	49	9
Female	47	0

No inversion is found exclusively in one sex in the populations of *C. dorsalis* which I have examined, but, unlike the other species, one of the inversions is found more often in one sex than in the other. The following figures are from combined samples from three different localities. The distribution may be accounted for by assuming that the inversion 1R is often linked in coupling with a dominant male-determining allele, or group

	Chromosome 1						Chromosome 2			Chromosome 4		
	1.1	1.1R	1.1S	1S.1R	1S.1S	1R.1R	2.2	2.2L	2L.2L	4.4	4.4a	4a.4a
Male	0	6	0	47	3	6	6	9	47	37	21	4
Female	1	1	5	10	21	0	1	9	28	18	16	4

of alleles, and that this arrangement is maintained by selection. The fact that all 1R.1R larvae have so far been males strengthens this view.

In one population of *C. dorsalis* I found a female larva heterozygous for a short reciprocal translocation between chromosome 1 (the 'sex-chromosome') and chromosome 2. There have been no previous reports of this type of aberration in any species of Chironomus.

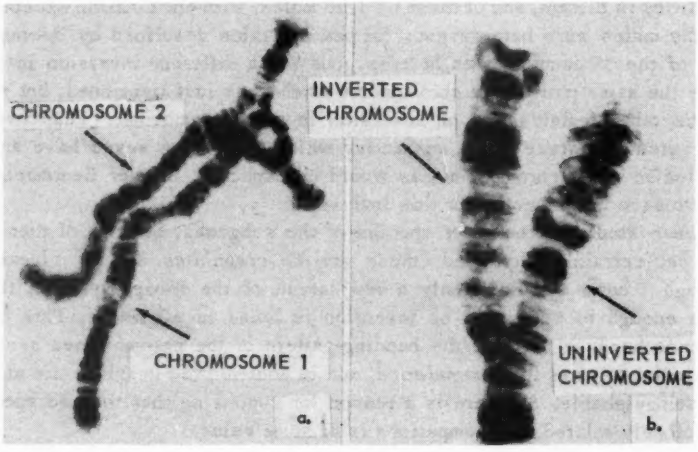

FIGURE 1. a. *Chironomus dorsalis*—Translocation, b. *Chironomus plumosus* (?) —Inversion found only in males.

These observations show that some inversions in *Chironomus* may be either in all males and no females; or they may be in some males and no females; or they may be more often in males than females. Further work may throw light on the problem of how the frequency of a Y-chromosome inversion in a population can be maintained in a stable equilibrium when the inversion occurs in some males, but not others.

LITERATURE CITED

Acton, A. B., 1956, Chromosome inversions in natural populations of *Chironomus tentans*. J. Genet., In press.

Beermann, W., 1955, Geschlechtsbestimmung und Evolution der genetischen Y-Chromosomen bei *Chironomus*. Biol. Zbl. 74: 525–544.

LETTERS TO THE EDITORS

Correspondents alone are responsible for statements and opinions expressed. Letters are dated when received in the editorial office.

AN EXPERIMENT ON EMPATHIC LEARNING IN DUCKS

It seems likely that certain instances of alleged mimicry require for their explanation the assumption that the potential predator can learn to avoid the dangerous model merely by observing an encounter of a congener with this model, without itself ever suffering the consequences of such an encounter. A possible instance of this would be the case of coral snakes (genus *Micrurus*) and their alleged mimics. Brattstrom has made an excellent case against striped, red, black and yellow snakes being true mimics, but others, notably Dunn, have resisted his arguments. It was this writer's belief that a telling criticism of Dunn's point of view lay in the fact that an encounter between a predator and a coral snake which might condition the former to avoid coral- and similarly marked snakes would be fatal to the predator. Either one must assume, as R. MacArthur (pers. comm.) has suggested, that an innate predisposition to avoid coral-snake-patterned reptiles has arisen via a chance mutation and selection, or that an unfortunate encounter between a predator and a Micrurid (unfortunate for the predator) would serve to teach other potential predators to avoid this prey. The latter possibility, either by itself or in conjunction with the former, seems eminently more plausible as an explanation than the former (Morgan). However it seemed unlikely, a priori, that many predators, particularly birds, would be capable of this kind of learning. This last assumption can now be regarded as false.

If an animal is conditioned to avoid a particular object, and a second animal who has either observed the conditioning process or else has established social relations with the first also avoids this object, without himself having been directly conditioned, we can speak of empathic learning having occurred. In the case of birds, this category of behavior can be due to at least four different mechanisma:

1. true insight
2. visual imitation
3. secondary conditioning
4. social facilitation

Together, these mechanisms probably account for the traditions so many birds, especially waterfowl (Hochbaum), manifest.

Evidence for true insight in birds is scant, and the reliability of cases that have been reported remains open to serious question. Cases of visual imitation are discussed by Thorpe. Secondary conditioning refers to the process where an auditory, or other, sign stimulus serves as the conditioning

stimulus for a second animal. Evidence for the existence of social effects strong enough to account for certain instances of empathic learning is provided by the experiment described below, which also provides a method for determining the existence of the other types.

For the first series of tests the apparatus consisted of a wire cage, two by three feet, which was surrounded by a second cage, three by four feet. Inside the inner cage were placed two feed dishes, one of which rested on a colored background and was surrounded by an electric grid connected to a source of 120 volt AC. A single Muscovy duck (*Cairina moschata*) was placed in each cage. Trials lasted from 10 to 25 minutes and were held on successive days. Of two ducks conditioned to avoid the wired dish, both learned to make the discrimination after two trials. Neither of these ducks, nor a third duck, showed any tendency to avoid the wired dish prior to the onset of the conditioning trials. The positions of the dishes, of course, were altered at random. Of the two ducks who served as observers (in the peripheral cage), one when positions were reversed, proved to have learned to avoid the wired dish. The second did not, but it must be noted that this was the only duck of the group that had not been hand-reared and was highly agitated when confined (see below).

The second series was identical to the above, except that semi-tame mallards (*Anas platyrhyncus*) were used in place of the Muscovies. These could not be conditioned or even accustomed to the apparatus. Thus, for the third series, a larger set of cages was constructed, the outer one measuring six by eight feet, the inner one having a diameter of three feet. This time the two dishes, the control and the wired dish, and the ducks, were left in the cage constantly, instead of being periodically introduced. After four days, the ducks in this compartment had been thoroughly trained to avoid the wired dish. Positions were reversed with the observer ducks, and these latter quickly indicated that they had not profited from their comrades' experiences. In this series, three ducks, two females and one male, had been in each of the two sections of the apparatus simultaneously.

Inasmuch as the ducks still appeared agitated even in this larger enclosure, a fourth series was conducted in which the conditioning was done in the open with the ducks unpenned. The observer trio (again, two females and one male) were enclosed in a six by eight foot pen which always provided a sight of the two feed dishes. A much longer time was required to condition the unpenned ducks, primarily because other sources of food were available to them. Consequently, they came to the feed dishes only as a last resort. After fourteen days, however, they appeared to be discriminating perfectly between the wired and unwired dish. Accordingly, the two dishes were removed, the observer ducks released, and 24 hours later the two dishes replaced. Positions were again chosen at random. Nonetheless, all of the ducks avoided the wired dish, even when snow cover made all other food supplies unavailable. They would peck corn off the ground directly beside the dish, but never stepped on the colored background which the grid surrounded.

Finally, for the fifth series, the three ducks who had been directly conditioned to avoid the wired dish were removed and replaced by a new trio. This group was again allowed 24 hours with the other ducks (the observer trio of series four) during which time the dishes were removed. Upon their re-introduction these new ducks, too, carefully avoided the wired dish. Tests with other ducks again demonstrated the absence of an innate disinclination to feed from the wired dish prior to the administration of a shock.

It is clear, therefore, that a kind of learning which has been termed social facilitation (Thorpe) can play a significant role in the behavior of social species of birds. Whether learning due to visual imitation or secondary conditioning can also occur can not be said on the basis of these experiments. By testing the observer birds in the absence of the conditioned group and by using a conditioned stimulus which is less likely to elicit innate sign stimuli than a severe shock (as proposed by J. King, pers. comm.), we expect to gain information about these possibilities as well. Finally, it should again by stressed that unnatural conditions (cf series two) are apt to provide misleading information about the learning abilities of wild animals.

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LITERATURE CITED

Brattstrom, B. H., 1955, The coral snake mimic problem and protective coloration. Evolution, 9, (2): (notes).

Dunn, E. R., 1954, The coral snake "mimic" problem in Panama. Evolution, 8, (2): 97–102.

Hochbaum, H. A., 1955, Travels and traditions of waterfowl, U. of Minn. Press.

Morgan, L., 1896, Habit and instinct, pg. 46–51, et al., E. Arnold.

Thorpe, W. H., 1951, The learning abilities of birds, Ibis 93: 1–52, 252–296.

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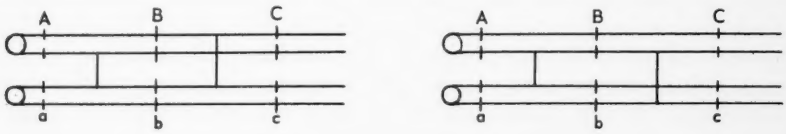
MODES OF TETRAD FORMATION

The letter under this title in a previous issue (Bennett 1956) prompts a few comments.

"Modes of tetrad formation" corresponds to my (Papazian 1952) "classification by N's, P's and F's" and is a good name. This classification has the virtue of reducing the number of classes and therefore the calculations, but one must consider how much baby is being thrown out with the bath water.

The amount of information lost was stated as being "at worst a failure to distinguish between the two types of 3-strand doubles." (Papazian 1952). These two types are shown below. In both cases A – B = F, A – C = F, B – C = F.



Whether the distinction between these two contains any information about crossing-over or any genetic information is the point at issue. Bennett holds that it does not and therefore believes that I do not know what classes I have myself enumerated. The point may seem a fine one but I think it could be a matter of considerable genetic importance to know on which of two genotypically different strands the multiple break occurred. If certain alleles, for instance, tended to make breaks occur in clusters one would expect the 0 and the 2-break strands to contain this allele and the two 1-break strands to contain its wild type counterpart.

Furthermore, the more sophisticated distinction between tetrads W,X;Y,Z and W,X;Z,Y is of significance to geneticists if not of genetic significance. This distinction has been used in two related ways. It has been used by Whitehouse (1942) to check on the very important point of whether the two centre nuclei after the second meiotic division pass each other in the ascus and it has been used by Whitehouse and Haldane (1946) to demonstrate that in *Neurospora sitophila* (but not in *Neurospora crassa*) there is an excess of asymmetrical post-reduction, the implication being, according to the authors, that the actual order of the 4 chromatids after terminalisation of chiasma in the first meiotic division is preserved all the way through the second meiotic division.

LITERATURE CITED

Bennett, J. H., 1956, Modes of tetrad formation. Am. Nat. 852:195–199.
Papazian, H. P., 1952, The analysis of tetrad data. Genetics, 37:175–188.
Whitehouse, H. L. K., 1942, Crossing-over in Neurospora. New Phytol. 41:23–62.
Whitehouse, H. L. K., and J. B. S. Haldane, 1946, Symmetrical and asymmetrical reduction in ascomycetes. Jour. Genet. 47: 208–212.

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